MODELING THE EFFECTS OF WORKER RULES ON TERRITORIAL CONFLICTS IN ANTS

by

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ABSTRACT

We investigate how worker rules and battle conditions affect the overall behavior of territorial battles, battle initiation, and community structure in ants of the genus *Tetramorium*. Battles are modeled with partial differential equations describing how workers move through the battle and return to the nest to recruit. The probability of battle initiation was investigated for different worker rules and initial conditions using a two-dimensional individual-based simulation. We extend the model for battles to find a distribution of territory sizes for a one-dimensional community and include a model for colony founding, growth, decline, and death. We find that the class of workers in the battle using information to make decisions affects battle dynamics with a Hopf bifurcation, where battles change from having steady state solutions to oscillations, occurring when 34% or more grappling workers are using information. Larger colonies are able to control more territory than the break even point proportional to colony size. Initial conditions followed by recruitment response have the strongest effect on the probability of battle initiation, suggesting that some outside stimulation may be required to initiate a battle. Total ants in the community are sensitive to the lifespan of the colony and how many workers survive from one year to the next. Diversity and total number of colonies were sensitive to recruitment rate and which ants used information in the battle with lower diversity and total colonies when recruitment is high and information is used by grappling workers in the battle.

For Staci and Abbi.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

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CHAPTER 1

INTRODUCTION

Territoriality is seen in many different species. This includes mammals (deer, antelope, squirrels, wolves, coyote, etc.) [6, 10, 33, 54], birds [49], fish [14], and social insects [27]. Often territorial behavior occurs in order to monopolize some resource such as nesting sites, food sources, or mating opportunities [2, 10, 25]. Intraspecific conflicts can lead to the death of losing combatants and the winner gaining control of the object of conflict [1, 55]. Some species have developed signals to indicate strength or fitness, eliminating the necessity of the loser being killed [24, 35]. The effects of territoriality can be seen in territory sizes controlled by combatants, opportunities to mate, and the overall community structure.

Territorial behavior causes changes in habitat. Wolf territories make it more likely to find deer in boundary areas where wolves are less likely to explore [33]. Arboreal ants usually have absolute territories and tolerate little to no heterospecific ants, leading to buffer zones between colonies. Ants engage in cooperative defense, but unlike vertebrates, decisions are made at the worker level and are not controlled centrally [16]. One species that establishes absolute territories with buffer zones is the weaver ant (*Oecophylla longinoda*) [25]. They will maintain large territories up to 1600m^2. Weaver ants rigorously maintain and patrol their borders and tolerate very few other species. Foreign conspecifics are rigorously excluded from their home territory to the point that this creates a "no ants land" between colony boundaries.

Ants have been compared to humans in the complexity and tendency of territorial behaviors [23, 36]. Examples of this complexity range from absolute territories where resources are uniformly distributed and continuously renewed, to spatio-temporal territories where resources are distributed in patches and finding them is unpredictable. When resources are unpredictable, territorial defense focuses more on resources than on actual

space [25].

Ants of the species *Myrmecocystus mimicus* have spatio-temporal territories. Colony territories overlap where workers from neighboring colonies would forage in the same area without confrontation. *M. mimicus* is a scavenger that preys on termites, collects floral nectar, and tend Hemiptera. When a rich food source such as a termite nest is found near a neighboring nest, workers recruit to the neighboring nest to interfere with their foraging by engaging stilt-walking display tournaments. In the event of large differences in numbers of workers from each colony (10 times or more) the stronger colony would raid the weaker colony, either drive off or kill the queen, and then incorporate all workers, honeypots, and brood into their own nest [24]. Other species that have ritualized territorial behavior and spatio-temporal territory is *Prenolepis imparis*. *Camponotus americanus*, the *Formica rufa* group, and *Iridomyrmex purpureus* all display ritualized defense of absolute territories [19, 27]. Palearctic ants of the genus *Tetramorium* stage large intraspecific battles with very little death in defense of absolute territories [37, 41, 47].

Territorial models typically fall into two categories: (1) partial differential equations (PDEs) developed using the underlying movement of the organisms being modeled or (2) statistical physics analyzing the individual movement and interaction of individual organisms. There are benefits and limitations to both types of models depending on whether the model is to make predictions at the cost of some of the underlying biology (PDE) or describe emergent phenomena from underlying mechanisms while losing the ability to make predictions (statistical physics) [40, 42].

An example of a mechanistic model is the model of wolf pack territories developed by Lewis and Murray in 1993 [33] where they created a system of PDEs where wolf movement was governed by two main rules: (1) movement was mainly dispersive while wolves search for food and move through the territory and (2) if a foreign scent mark is encountered, the wolf will move toward some central point in the territory and it will increase its own scent marking. The models predict higher density of scent marks at the boundary rather than the center of territories, which is supported by data. Stable steady state solutions give rise to territories. It was shown that deer should be mainly found in the boundary between the two packs. This model was fit to coyote radio telemetry collected in Yellowstone National Park and another PDE territorial model with no flux boundary

conditions because coyotes have similar marking patterns and territories as wolves [40].

Other models focus on conflicts rather than territory; one of these is Lanchester's equations. Lanchester's equations were developed after World War I to model battles of attrition between two armies. It has been applied to conflicts involving humans [18], chimpanzees [55], and birds [49]. In 1993, Franks and Partridge [20] first suggested using Lanchester's equations for applications to ants. There are two laws that describe different scenarios. (1) The square law allows for groups to act cooperatively to attack and kill individual opponents. One group will defeat the other if the product of its fighting abilities and the square of the army size is larger. (2) The linear law models conflicts when there is no added benefit from concentration. In the linear law, the winning group has to have a larger product of fighting ability and size of army. Fighting ability of soldiers has a much larger effect on the outcome of the battles [4]. Even though there is widespread use of Lanchester's equations, they do not allow any predictions on territory size.

In their paper in 1980, Hölldobler and Lumsden [25] address different types of ant territories. They propose using economic models to describe territories where benefits from the territory balance out with the costs of maintaining territories. Boundaries will occur where benefits and costs are equal. Similarly fire ant (*Solenopsis invicta*) territories have been modeled by quantifying the pressure exerted by each colony at the edge of the territory and boundaries formed when pressure from competing colonies was balanced [3].

In our models, we use behavioral rules of ants in the genus *Tetramorium* for modeling behavior of workers in battles. Our models are used to investigate how those rules in territorial conflicts affect how battles progress and territory size, the initiation of battles, and overall community structure involving neighboring nests of *Tetramorium*.

We refer to ants of the genus *Tetramorium* since it is difficult to determine individual species [48]. They are known commonly as the pavement ant for their prevalence of living underneath roads and sidewalks [36] and are introduced species with native ranges in Europe and Asia [13, 52]. Pavement ants are generalists in their preferred food sources, making use of hemipterans, harvesting seeds, preying on other insects, and making use of most human foods [11]. Territorial conflicts in the pavement ant are conducted with very little loss of workers participating in battles. In the spring when workers are beginning

to leave their nests, there is no memory of old territories or knowledge about how neighboring colonies fared over winter. Workers from neighboring nests encounter each other because no borders exist and encounters lead to battles. Battles can last up to three days and involve thousands of workers. After battles have ended, workers of each colony will have learned where the territorial boundary exists and there is an establishment of buffer zones. The boundaries are usually stable for the rest of the year [37, 41, 47]. Observations of pavement ant battles in the United States go back for over 100 years [37]. In studies of nesting sites, Sanada-Morimura et al. in 2006 [47] found that *Tetramorium* ants are limited by soil temperature, preferring sunny nesting sites. The best brood maturation rates in the lab matched sunny areas in the field (based on temperature). Perhaps the most important factor in territory size is colonies that have larger territories tend to produce more sexual offspring [11, 47].

Plowes in 2008 [41] mapped out several *Tetramorium* colony borders through the use of baits. Battles were instigated in the field by inducing encounters between non-nestmates using baits. When two workers from separate colonies first encounter each other, baits were removed. After grappling for a time, workers returned to their respective nests to recruit nestmates to battle. During battles, ants searching in the battle will encounter other non-nestmate ants and form grappling pairs. As workers are grappling, other searching ants will make contact with dyads before moving on (Figure 1.1). Workers will leave and recruit nestmates to the battle through pheromone trails and leading groups back to the battle (personal observations). Oscillations in the spatial locations of battles were recorded where bouts of recruitment from opposing colonies would push the battle back and forth between colonies [41]

In this thesis, we investigate how worker rules affect three aspects of territoriality and intraspecific battles: (1) What are the worker rules that will cause our model to have similar dynamics to those observed in personal observations and those reported in [41] and how does that affect territory controlled by each colony (battle model) (2) Which worker rules affect the initiation of battles (battle initiation) (3) What role do worker rules play in the overall structure of a community of pavement ant colonies (community model). Each of these questions has different scales in either the number of ants involved, distances, or the dimensions (Figure 1.2).

1.1 Chapter Introductions

The natural order of chapters would be to start with the question involving the smallest number of ants and work our way up to the question with the largest number of ants. We present our work in the order of the questions above because developing a model to describe battles was the first step in approaching each of the questions. The framework of the battle model provided inspiration and direction in answering the battle initiation and community questions.

1.1.1 Chapter 2 (Battle Model)

In this chapter, we investigate what worker rules are necessary for battles to have the dynamics observed in [41], especially how battles can oscillate with recruitment. A sensitivity analysis was performed on the parameters in the model to determine which worker rules, as described by the parameters, were best for colonies of different size. The scale in this question is one-dimensional with hundreds to thousands of ants in battles.

A partial differential equation model using coupled one-dimensional advection equations was used to describe ant movement in the battle. Ants were able to switch between different roles in the battle including traveling, searching, fighting, and returning to the nest to either recruit or leave the battle. Two classes of nest ant were modeled and they are recruitable ants and leader ants recruiting nestmates to return to the battle. Testing the effects of information collection and decision making on battles was investigated by allowing decision making to change between searchers and fighting ants.

1.1.2 Chapter 3 (Battle Initiation)

In this chapter, we investigate what initial conditions and worker rules lead to initiation of battles. Battle initiation was investigated by using a two-dimensional agent-based model for ants in similar classes to the battle model. Workers could be traveling to the battle, searching the battle area using a correlated random walk, fighting, and returning to the nest to become either nest ants or to recruit nestmates into the battle. The two classes of nest ants are recruitable ants and leaders. The scale of this question is tens of ants and two dimensions.

We ran multiple simulations of the agent-based model for different parameter values

while recording whether or not battles begin. The probability of battle initiation was determined by dividing the total number of simulations for each parameter value into the number of successful battle initiations. The main rules investigated were recruitment rate of leaders, rate at which leaders switch to traveling and recruitable ants, how long ants remain fighting, and the probability of fighting. Effects of the size of battle area and different initial conditions on battle initiation were investigated.

1.1.3 Chapter 4 (Community Model)

This chapter is similar to Chapter 2 in that it is one-dimensional, but the battle model is used to solve for territory size of multiple colonies in a community. Territory size allows us to couple the battle model with a model describing how colonies grow or decline depending on how much territory they are able to control at the start of each season. Coupling colony growth and the battle model allowed us to investigate what the effects of worker rules are on the overall structure, colony diversity (colony size versus combined total of ants for all colonies), and colony sizes in the community.

Rules investigated are: which class (searching or fighting) collects information and makes decisions, and different recruitment rates. Death rates of colonies and worker ants were also changed to see how they would affect the community.

1.2 Motivation

A partial differential equation model describing information collection and territorial rules that ant workers follow in territorial conflicts has never been done. This work has allowed us to investigate questions in intraspecific territoriality including what worker rules most affect territory size and how battles progress. This also allows us to make predictions on how communities are structured and what role worker rules plays in those.

This system is ideal to work with since it is very easy to find ants and colonies to study. For most of the United States, they are outside on the sidewalk [52]. This opens up opportunities for citizen science projects involving *Tetramorium* ants in the future.

Figure 1.1. Pavement ant battle along along a seam in the pavement of a sidewalk.

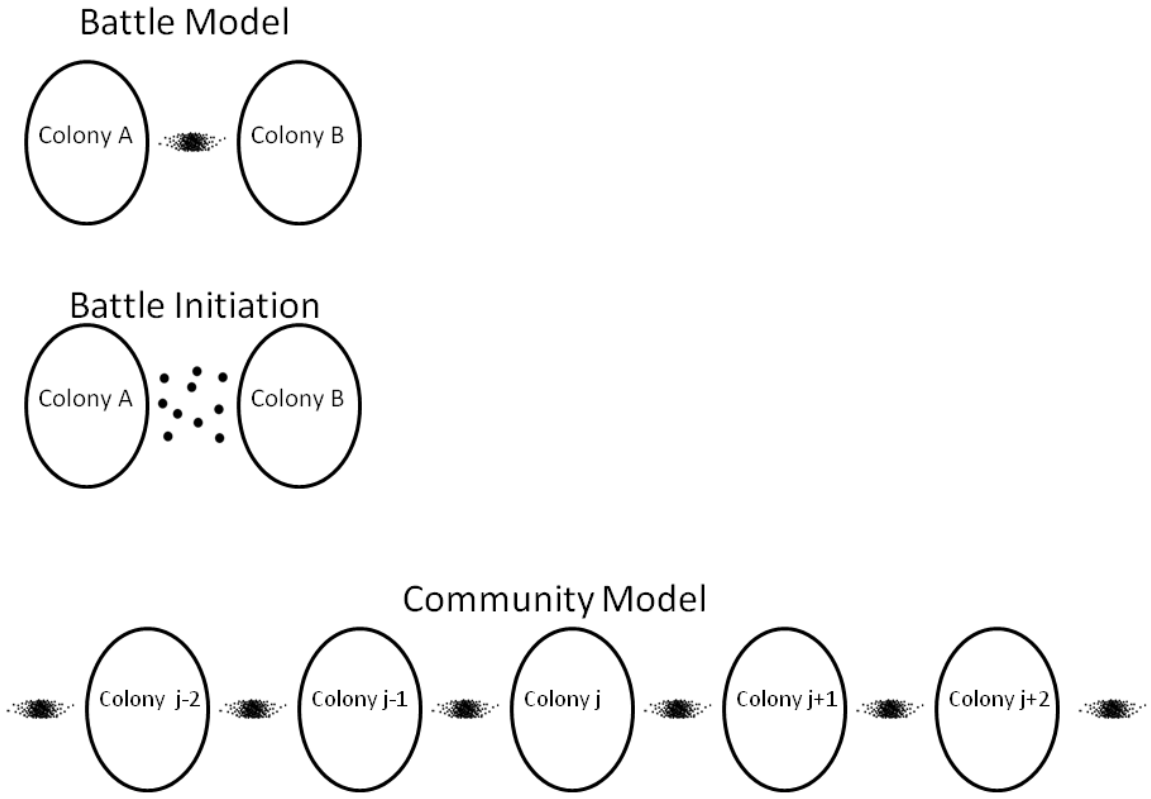

Figure 1.2. Scale of the three models in the thesis. In the battle model, there can be hundreds to thousands of ants in the battle and it is modeled in one dimension. In the battle initiation model, there are only tens of ants involved and it is modeled in two dimensions. For the community model, there are up to tens of thousands of ants involved in all of the battles and it is modeled in one dimension.

CHAPTER 2

THE EFFECTS OF WORKER RULES ON ANT BATTLES

We develop a partial diferential equation (PDE) model for territorial conflict in ants of the genus *Tetramorium*. There are a total of 15 classes of ants, 7 for each colony, and 1 describing the fighting in the battle arena. The seven states for each colony are the same except for direction of travel in the battle area. A stability analysis on the parameters was performed finding that, in all realistic cases, larger colonies control more territory than the break even point proportional to colony size. The model has two Hopf bifurcations, one when information collection changes from searching ants to dyads grappling non-nestmate ants in battles and the other when the duration of dyads is reduced to an average of 0.26 minutes.

2.1 Introduction

Competition for territory occurs in many animals such as red squirrels [54], coyotes [7], wolves [33], and ants [27]. Antagonists participate in mortal contests or ritualized displays with some type of signaling or some combination of both [19]. Types of territory for ants can also differ, ranging from absolute defense of boundaries to ritualized combat to defend temporary resources [25]. During territorial conflicts in groups, the larger group usually takes more of the territory [1, 7]. In territorial conflicts involving ants, decisions are not made at the colony level but at the worker level in the form of rules each worker follows [16].

Ant workers have been shown to posses several abilities. Among those are the ability to count their steps when searching their territory [56] and identify nest and non-nestmates through contact and pheromones [27]. Contact experiences with nest and non-nestmates are stored in the brains of some ants, allowing workers to know if they have had contact more with nestmates or non-nestmates in a recent interval. Recent contact can lead to

decision making and worker responses during territorial conflicts [28].

When ants need help with collecting food or defense from nestmates, they will return to the nest or other location where workers are assembled and recruit additional workers. Recruits can be led to the location of interest by either group recruitment or pheromone trails. Group recruitment is performed when a recruiting worker leads a small group of ants, which usually stay close or in contact with the leader during the return to the area of interest. Pheromone recruitment allows individual recruits to leave the nest and follow a chemical trail leading to the area of interest [16]. Information can be communicated by either modification of the environment (pheromone trails etc.) or directly by contact [5]. Collignon and Detrain in 2010 [16] show that leader ants are able to modify their recruitment based on the quality of the available food source.

During their ritualized combat, *Myrmecocystus mimicus* workers will have stilt walking competitions with non-nestmates from neighboring colonies [25]. Pavement ants (*Tetramorium caespitum*) are known for staging large battles along sidewalks and other man made structures [37], leading to battles that are quite linear (Figure 2.1). Battles can last for hours and often will have oscillations due to bouts of recruitment from workers in battles. Workers will create grappling pairs (dyads) while searchers from both colonies initiate contact with dyads [41].

Mathematical modeling in territoriality has been done in wolves using partial differential equations to model interactions with wolves and deer [33], and many other animals and methods including individual-based modeling [43]. Modeling of ant territoriality has been done with ordinary differential equations in the form of Lanchester's laws [4, 20], using a cost benefit analysis [25] or economic model where neighbors establish territories based on some balance of either signaling or marginal value of territory gain that is equal [1].

While some ants actively patrol territorial borders and maintain enough workers for defense such as *Azteca trigona* and *Oecophylla longinoda* [1, 25], some species such as *Tetramorium caespitum* rely on recruitment at the nest to defend territory [41]. A model of partial differential equations used to model ants traveling to the area of territorial conflict and back to the nest to recruit workers is lacking.

This paper uses partial differential equations to study how worker rules affect battle

progress in one dimension. We find which worker rules lead to oscillations in the battle as seen by Plowes in 2008 [41] and perform a sensitivity analysis on all parameters in the model to test which worker rules most affect territory size determined by battles. Recruitment is performed at the nest by workers that return from the battle. Workers use information gathered in the battle to then make decisions about what they should do in response to battle conditions. We also investigate how information is collected by workers and how changing worker's method of collection affects battle dynamics.

2.2 Methods

Our model tracks ants from two colonies that fall into three broad categories: ants in the nest, ants traveling from between a nest and the battle, and ants at the battle. We model nest ants (4 total) with ordinary differential equations (ODEs), and traveling ants (6 total) and ants in the battle (5 total) using partial differential equations (PDEs). There are 7 categories of ants for each colony plus 1 for interacting dyads for a total of 15 equations. Of these 11 are PDEs that keep track of positions of ants including dyads from each colony, traveling ants, ants in the battle searching for non-nestmates, and ants that return to the nest in either a motivated or unmotivated state. The remaining 4 equations are ODEs and track the leader and recruitable ants in each nest. Information spread is modeled in the nest as infectious disease spread [12] where recruits leave and travel to the battle on their own as if they were following a pheromone trail. No form of group recruitment was modeled.

When an ant is recruited, it becomes a traveling ant and moves to the battle for some minimum distance h. After passing the distance h, it switches to searching with the rate δ_t. Once in the searching class, ant movement is modeled using a velocity jump process where ants switch between moving away from the nest (leaving) and moving toward the nest (returning) at rate σ.

Searching and dyadic ants are collecting information and are able to make decisions. Because dyads and searching ants can choose to become unmotivated or motivated, this is where the information is collected. Information collection is regulated by the use of the parameter ϕ. When $\phi = 0$ then all information is collected by searchers and when $\phi = 1$ all information is collected by dyads. The model was tested to see how the parameter ϕ affected model behavior. The information collected by searchers and dyads is the ratio of

non-nestmates to nestmates that are within a radius of detection ω. Ratios are calculated using equations (2.1) where A_s and B_s are the total number of searching ants from colony A and colony B that make contact with either the searcher or dyad and are found by integrating over all searching ants a_{ls} and a_{rs} for colony A and b_{ls} and b_{rs} for colony B. We add ϵ to the numerator and denominator of the ratio equations to keep them from being undefined in the event that no ants make contact with searchers or dayds.

$$\begin{aligned} A_s(x) &= \int_{-\infty}^{\infty}(a_{ls} + a_{rs})e^{-\omega|y-x|}\,\mathrm{d}y \\ B_s(x) &= \int_{-\infty}^{\infty}(b_{ls} + b_{rs})e^{-\omega|y-x|}\,\mathrm{d}y \\ r_a(x) &= \tfrac{B_s+0.001}{A_s+0.001} \\ r_b(x) &= \tfrac{A_s+0.001}{B_s+0.001} \end{aligned} \tag{2.1}$$

Searching ants form dyads with non-nestmates when they encounter them with the mass action term α. Searchers can also become an unmotivated or motivated returning ant with a base returning rate of δ_s following equations (2.2). The probability of becoming motivated is given by $G_m(r)$ and the probability of becoming unmotivated is given by $G_u(r)$ where r, A_s and B_s are calculated by equations (2.1). The parameter k is a scaling factor for behavior of ants leaving dyads, m is the shape parameter of a Hill function and m_s is a scaling factor for total ants.

$$\begin{aligned} G_m(r) &= (A_s + B_s + 1)^{m_s}\left(\tfrac{r^m}{k^m+r^m}\right) \\ G_u(r) &= \left(\tfrac{1}{A_s+B_s+1}\right)^{m_s}\left(\tfrac{k^m}{k^m+r^m}\right) \end{aligned} \tag{2.2}$$

When dyads break up, the ants have three possible choices: (1) become an unmotivated ant and return to the nest and transition into a recruitable ant, (2) become motivated and return to the nest as a leader ant, or (3) return to the searching class. This is modeled with equations (2.3) where r is the same as in equations (2.1) and $F_u(r)$ is the probability of becoming unmotivated, $F_m(r)$ is the probability of becoming motivated, and $F_s(r)$ is the probability of becoming a searcher. The parameter k is a scaling factor for behavior of ants leaving dyads, m is the shape parameter of a Hill function, and c_m and c_u are the relative propensities to be unmotivated and motivated, respectively.

$$\begin{aligned} F_u &= \tfrac{c_u k^m}{k^m+r^m+c_m r^m+c_u k^m} \\ F_s &= \tfrac{k^m+r^m}{k^m+r^m+c_m r^m+c_u k^m} \\ F_m &= \tfrac{c_m r^m}{k^m+r^m+c_m r^m+c_u k^m} \end{aligned} \tag{2.3}$$

Ants that return to the nest as either a returning searcher or an unmotivated ant become recruitable ants. Those that return to the nest as motivated ants become leader ants in the

nests, which then recruit recruitable ants to the battle at rate ρ. Leader ants leave the nest with rate γ_l and lose motivation with rate δ_l.

Because ants from colony B follow the same rules, the equations differ only in the direction of travel and use of r_b instead of r_a. The full set of equations for ants in colony A are

$$
\begin{array}{ll}
\text{Traveling} & \frac{\partial}{\partial t}a_t = -V\frac{\partial}{\partial x}a_t - \delta_t a_t \\
\text{Leaving Searching} & \frac{\partial}{\partial t}a_{ls} = -V\frac{\partial}{\partial x}a_{ls} + \delta_t a_t + \sigma_r a_{rs} + \beta\delta_D(\phi F_s(r_a)+ \\
 & \qquad (1-\phi))f - \alpha a_{ls}b_{ls} - \sigma_l a_{ls} - \\
 & \qquad \delta_s(1-\phi)\left(G_u(r_a) + G_m(r_a)\right)a_{ls} \\
\text{Returning Searching} & \frac{\partial}{\partial t}a_{rs} = V\frac{\partial}{\partial x}a_{rs} + \sigma_l a_{ls} + (1-\beta)\delta_D(\phi F_s\left(r_a\right) + \\
 & \qquad (1-\phi))f - \alpha a_{rs}b_{rs} - \sigma_r a_{rs} - \\
 & \qquad \delta_s(1-\phi)\left(G_u(r_a) + G_m(r_a)\right)a_{rs} \\
\text{Returning Unmotivated} & \frac{\partial}{\partial t}a_{ru} = V\frac{\partial}{\partial x}a_{ru} + \phi\delta_D F_u\left(r_a\right)f + \\
 & \qquad \delta_s(1-\phi)G_u\left(r_a\right)\left(a_{rs}+a_{ls}\right) \\
\text{Returning Motivated} & \frac{\partial}{\partial t}a_{rm} = V\frac{\partial}{\partial x}a_{rm} + \phi\delta_D F_m\left(r_a\right)f + \\
 & \qquad \delta_s(1-\phi)G_m\left(r_a\right)\left(a_{rs}+a_{ls}\right) \\
\text{Recruitable Ants} & \frac{\mathrm{d}A_n}{\mathrm{d}t} = Va_{ru}(0,t) + Va_{rs}(0,t) + \delta_l A_l - \rho A_l A_n \\
\text{Leader Ants} & \frac{\mathrm{d}A_l}{\mathrm{d}t} = Va_{rm}(0,t) - \delta_l A_l - \gamma_l A_l \\
 & \\
\text{Dyads} & \frac{\partial}{\partial t}f = \alpha\left(a_{ls}b_{ls} + a_{rs}b_{rs}\right) - \delta_D f
\end{array}
\tag{2.4}
$$

Each colony has two boundary conditions. All ants that leave the nest from either the recruitable class or the leader class go into the traveling class of ants. Ants that reach the other nest are reflected back into the area between the two nests.

$$
\begin{array}{ll}
\text{Boundary Conditions:} & \\
\text{A ants:} & a_t(0,t) = \frac{1}{V}\left(\rho A_l A_n + \gamma_l A_l\right) \\
 & a_{ls}\left(X,t\right) - a_{rs}\left(X,t\right) = 0 \\
 & \\
\text{B ants:} & b_t(X,t) = \frac{1}{V}\left(\rho B_l B_n + \gamma_l B_l\right) \\
 & b_{ls}\left(0,t\right) - b_{rs}\left(0,t\right) = 0
\end{array}
\tag{2.5}
$$

The system of equations was solved numerically using the ReacTran package in R [51]. Stability analysis was performed by running the model for each parameter in a range from half to double the usual value. Key model outputs that were recorded are the mean location of the battle (the center of mass of the dyads) and whether or not the location oscillates, dynamics of battle, size of the battle in both number of ants and width, and the quantiles of the location of the mass of ants to characterize shape. For a list of parameters and their most used values, see Table 2.1. Parameters were used to match [41] where

available and the recruitment rate ($\rho = 0.002$) is based off of the recruitment rate described by Bonabeau et al. in their paper in 1998 [9].

2.2.1 Calculation of ω

The parameter ω (equations (2.1)) is the inverse of radius of detection around the dyad. This effective radius of detection will be much longer than the contact distance between individuals because it is summed over the full duration of the dyad. To determine the value of ω, we ran individual-based simulations to count how many ants from each colony made contact with dyads and found which value of ω fit the best. Parameter values in the individual-based simulation were kept the same as Table 2.1 except for δ_D. In order to reduce the noise in counting ants making contacts caused by the variation in dyad duration, we force dyads to persist for their averaged time of 1 minute. The value of $\omega = 0.14$ had the best r-squared value at 0.2632. Because these count data are Poisson distributed in both horizontal and vertical directions, we found the r-squared values with a perfect fit to be 0.44. The observed r-squared with $\omega = 0.14$ is thus 59.8% of the best possible r-squared value.

2.3 Results

We found steady state solutions to predict how much territory each colony will control after a battle has terminated. Searching ant densities peaked on the side of the dyad's center of mass nearest to their own colony (Figure 2.2). With colonies of equal size, the center of mass of dyads lie exactly on the center, but closer to the smaller colony otherwise. We studied how the center of mass of dyads changed with the parameters, finding that it moves toward the smaller colony for larger values of α, σ, δ_s, δ_l, ρ, and c_m and away from the smaller colony with larger values of V, β, and δ_D (Figure 2.3).

Increasing the intercolony distance X has effectively no change in the percentage of territory held by the larger colony ($N_A = 1000$, $N_B = 500$), which was 78.0%.

The total size of the battle decreases with larger values of δ_D, δ_s, X, and m_s (Figure 2.4) and increases with larger values of α, δ_l, γ_l, and k (Figure 2.5). The battle has a maximum size for intermediate values of V, β, and m (Figure 2.6). The parameters σ, ρ, c_u, and c_m essentially had no effect on the steady state size of battles.

The model is capable of sustained oscillations in location and size of the battle, as observed by [41]. We illustrate the effects of the information parameter ϕ as it changes information and decision making from searching ants to dyads (Figure 2.7) and δ_D (Figure 2.8) on switching between oscillations and steady states with oscillations predicted for $\phi > 0.347$ and $\delta_D > 3.84$. For $\phi = 1$ and $\delta_D = 1$, we studied other parameters that affect the magnitude and the mean position of the center of mass of the battle (Figure 2.9). In the oscillatory regime, the center of mass moves toward the larger colony as σ increases, which was the opposite of the situation seen in steady states.

Oscillations in location were not the only form of oscillation seen in the battle. Total mass in the battle would oscillate as workers would recruit. Again the main parameter that affected battle dynamics was ϕ. Figure 2.10 is a bifurcation diagram showing how mass of the battle was affected by ϕ. Not only did the battle oscillate as ϕ increased, but the total mass of ants in the battle decreased. The reduction in total ants grappling as ϕ increases is a result of more dyads leaving the battle motivated or unmotivated and traveling to their nests. Other parameters that affected oscillations in the battle are β, α, σ, δ_l, γ_l, c_u, and k. Oscillations were reduced as β and α increased, but the opposite was true for σ, δ_l, γ_l, c_u, and k (Figure 2.11).

The period found for oscillations in location and total ants in battles ranged from 20 minutes when $\phi = 0.388$ to 15 minutes when $\phi = 1$. This corresponds with the period of about 20 minutes found in *Tetramorium* battles [41]. Oscillations in battles move back and forth between points closest to each colony (Figure 2.12). The peak in total ants coincides with the location of the battle being closest to the larger colony while the fewest ants occurs when the battle is at the closest position to the small colony. All oscillations for location of the center of mass of searching ants from each colony and the dyads are in sync, but oscillations for total searching ants from the larger colony and dyads are out of sync with oscillations in total searching ants from the smaller colony by 180° (Figure 2.13). The smaller colony is like "prey" responding to changes in "predator" numbers (larger colony) in predator prey systems.

2.4 Discussion

We have developed a PDE model for territorial conflict between neighboring ant colonies. The model tracks two classes of ants in the nest, recruitable ants and leaders, while tracking six classes of ants in the battle: traveling, searching away from and toward the nest, dyads, returning motivated and unmotivated. By defining the boundary between two colonies in the battle to be the center of mass of the dyads, territory controlled after the battle can be predicted. In every case, the larger colony controls more territory than if territories were divided up evenly based on colony size. This bias is smaller when the distance between colonies is larger. Although some parameters were able to move the center of mass back toward the larger colony, only increasing β to nearly 1 was sufficient to approach an even division. This is not a realistic case because all workers transitioning from dyads to searching ants would move away from their own nest.

The information parameter ϕ adjusts whether searching ants ($\phi = 0$) or ants in dyads ($\phi = 1$) make decisions, giving two alternative hypothesis about the feedback that controls in the overall dynamics of the battle. As ϕ increases from 0 to 1, more decisions are being made by dyads creating delay in the model causing a Hopf bifurcation when just over a third of decisions are being made by dyads ($\phi > 0.347$). Our models predict that if a battle is oscillating, then at least a third of the decisions about recruitment and leaving the battle unmotivated will occur in the dyads.

Increasing δ_D diminishes and eventually stops oscillations since it reduces the delay in the model by reducing a worker's time spent in a dyad. The reduction in the delay is strong enough that the model has a Hopf bifurcation when $\delta_D > 3.84$ even when $\phi = 1$.

Oscillations in location and mass of battles were not affected by the other parameters except for the location of the oscillations, which got smaller for larger values of σ. Since σ controls how ants switch their directions from leaving to returning, we would expect fewer searching ants to make it to the other side of the battle, reducing the mean center of mass of the dyads.

This model could use corroboration from an individual-based model to see if ants behaving with individual behaviors can approximate model solutions. It could be done in a single dimension and would have to be at the diffusion limit to compare results.

Most ant battles, even those for *Tetramorium*, do not just happen on a straight line. They

will expand out in two dimensions (Figure 2.1). Eventually to accurately model battles in ants, it will be useful to have models written in 2 dimensions.

Group recruitment was not considered by this model. How would groups of workers arriving to a location in the battle at one time affect the dynamics of the battle? Perhaps this might give the smaller colony the chance to gain back more territory since group recruitment is inefficient where in pavement ants, only 50% of recruits in groups make it to the location their leader takes them [17]. This may allow the smaller colony to possibly have more success than the larger colony in getting its group recruits to the battle.

With our PDE model, we were able to show that oscillations in location and mass of ants are possible in ant battles if enough information is collected by dyads as long as there is a long enough duration of the dyads. Larger colonies are expected to gain more territory than the break even point proportional to colony size.

Table 2.1. Parameters in the battle model.

Parameter	Description	Value or Range
	Parameters That are Only in the Nest	
δ_l	Rate at which leaders become unmotivated	0.25/min
γ_l	Rate at which leaders leave the nest	0.25/min
ρ	Recruitable ants leave for the battle	0.02/min/ant
	Parameters in the PDEs	
V	Speed of ants	0.6 m/min
δ_t	Rate at which traveling switch to searching	4-6/min
σ	Searcher switching rate	0.1/min
β	Proportion of dyads that go to leaving searchers	0.5
δ_D	Rate at which dyads break up	1/min
α	Rate at which dyads are formed	0.3 m/(ant min)
ϕ	Information parameter	0-1
δ_s	Basic leaving rate for searchers	0.1/min
	Parameters in the $F(r)$ and $G(r)$ functions	
k	Scaling factor in functions for post-dyadic behavior	2.0
m	Shape parameter for post-dyadic behavior	1-3 (1)
c_u	Relative propensity to leave dyad unmotivated	1.0-3.0 (1.0)
c_m	Relative propensity to leave dyad motivated	1.0-3.0 (3.0)
m_s	Scaling factor for total ants	0.25
ω	Radius of perception for searchers and dyads	0.14/m
	Other Parameters	
X	Distance between nests	2-4 m
h	Minimum distance of traveling class	$0.05X$

Figure 2.1. Battle involving two colonies of *Tetramorium* ants.

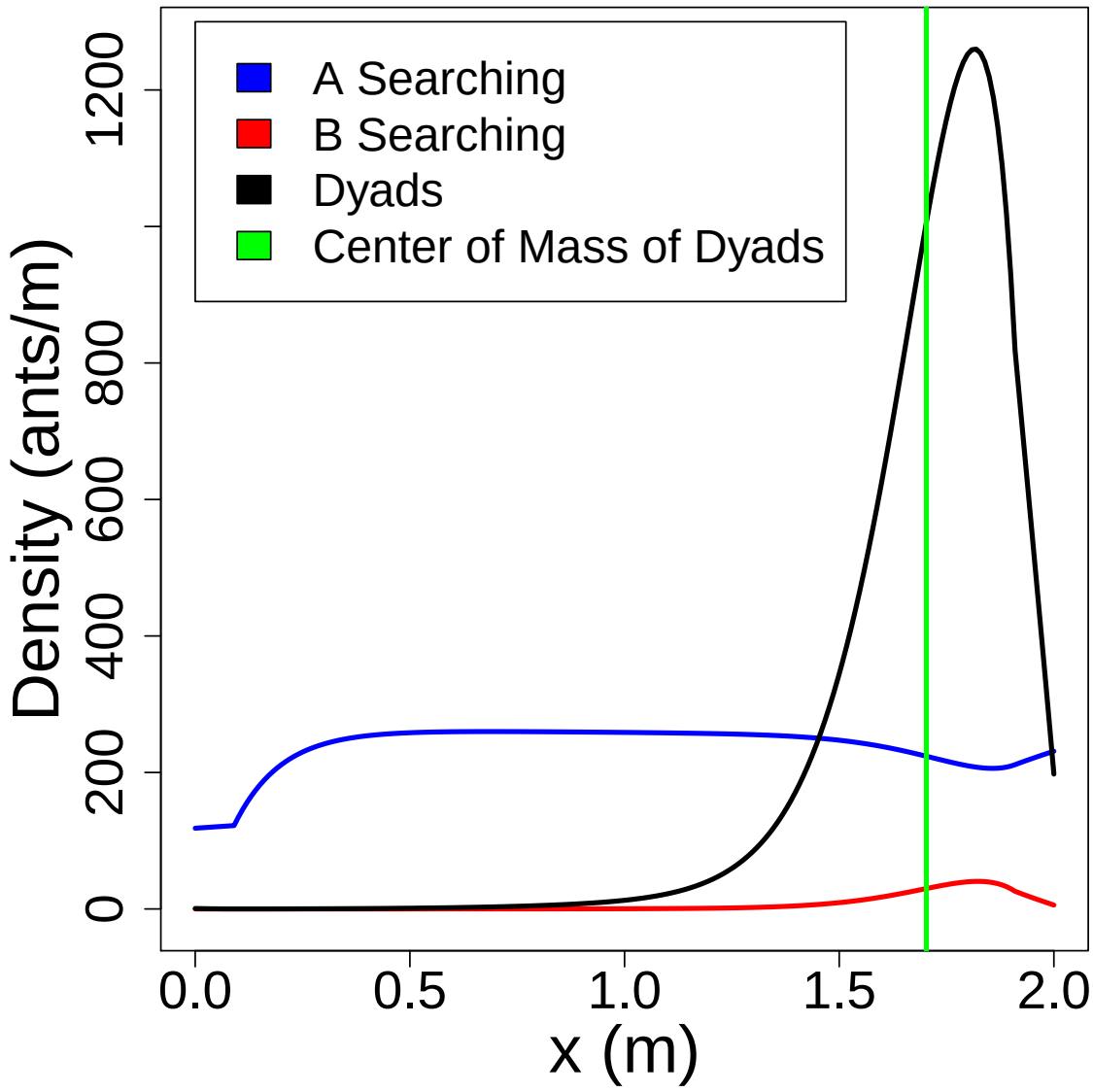

Figure 2.2. Model steady states for searching ants and dyads with the center of mass of dyads shown by the vertical green line. There are 1000 ants in colony A and 500 ants in colony B. Parameter values as in Table 2.1.

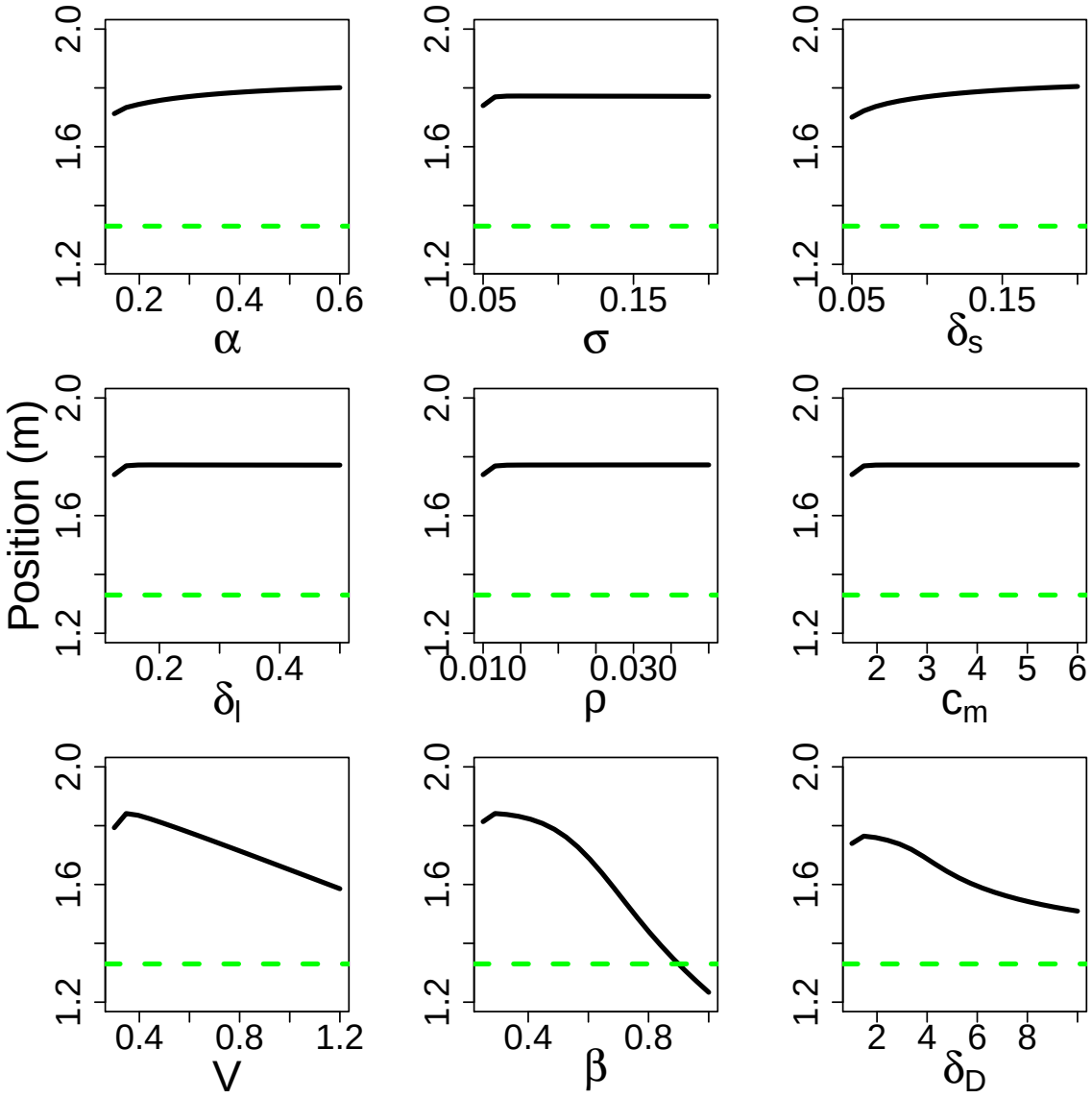

Figure 2.3. Location of center of mass of the battle over a range of parameter values. The green dashed line ($y = 1.33$) shows the break even point proportional to colony size. Colony A at $x = 0$ has 1000 ants and colony B at $x = 2$ meters has 500 ants. All other parameters are as in Table 2.1.

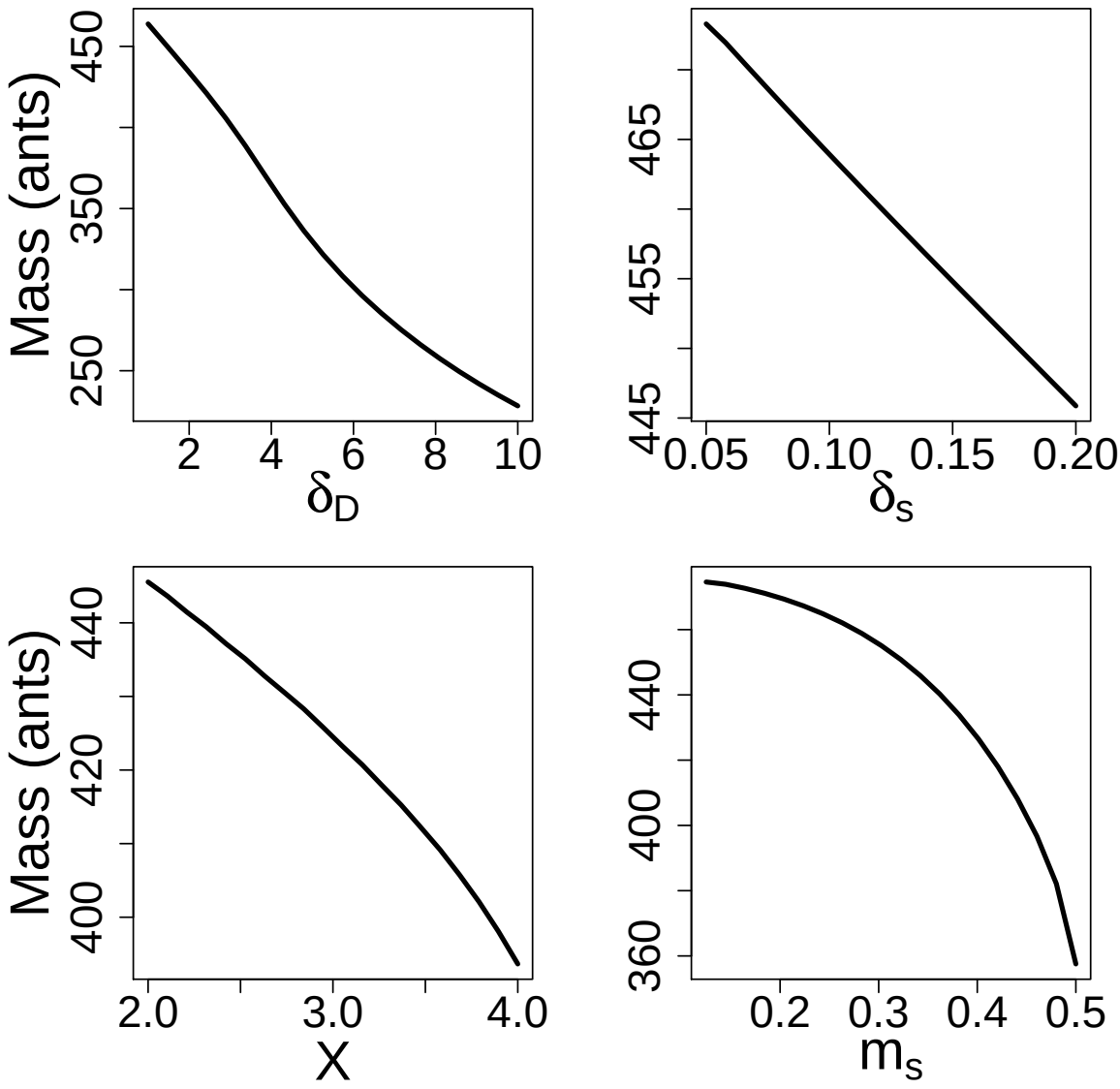

Figure 2.4. Total number of dyads at steady state decreases as δ_D, δ_s, X, and m_s increase. Colony A has 1000 ants, and Colony B has 500 ants. All other parameters as in Table 2.1.

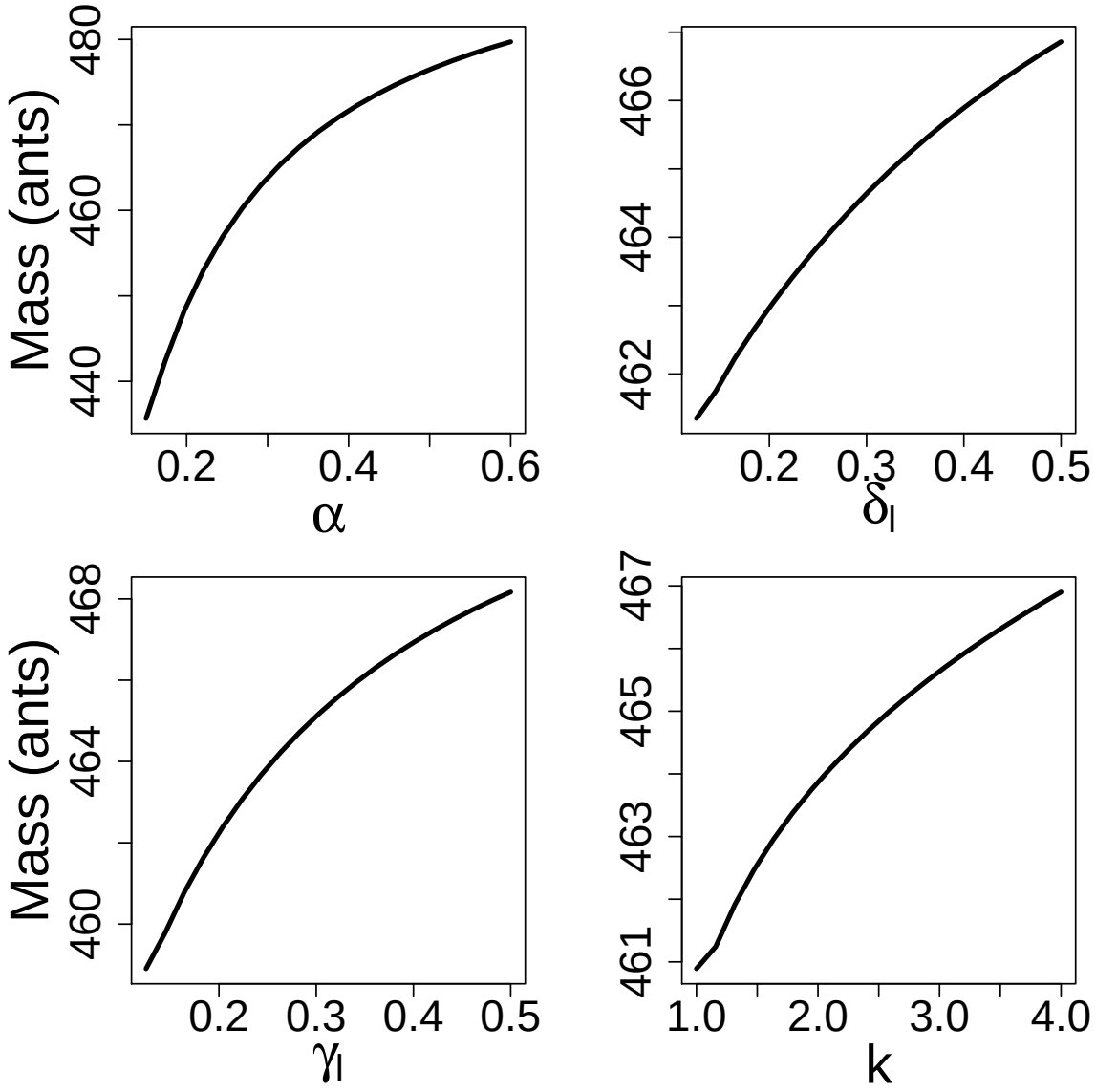

Figure 2.5. Total number of dyads at steady state increases as α, δ_l, γ_l, and k increase. Colony A has 1000 ants, and Colony B has 500 ants. All other parameters as in Table 2.1.

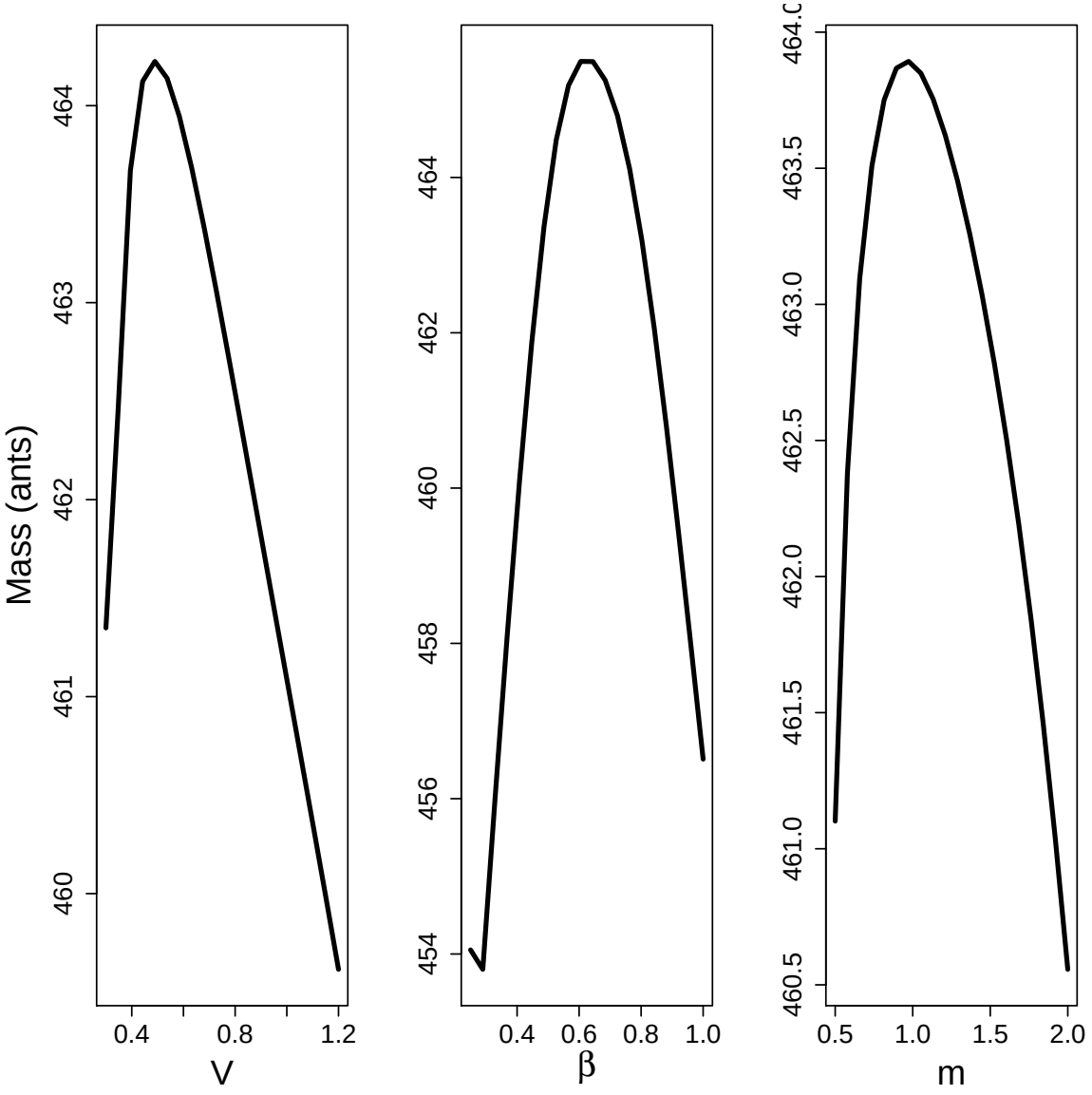

Figure 2.6. Total number of dyads at steady state has a maximum for intermediate value of V, β, and m.

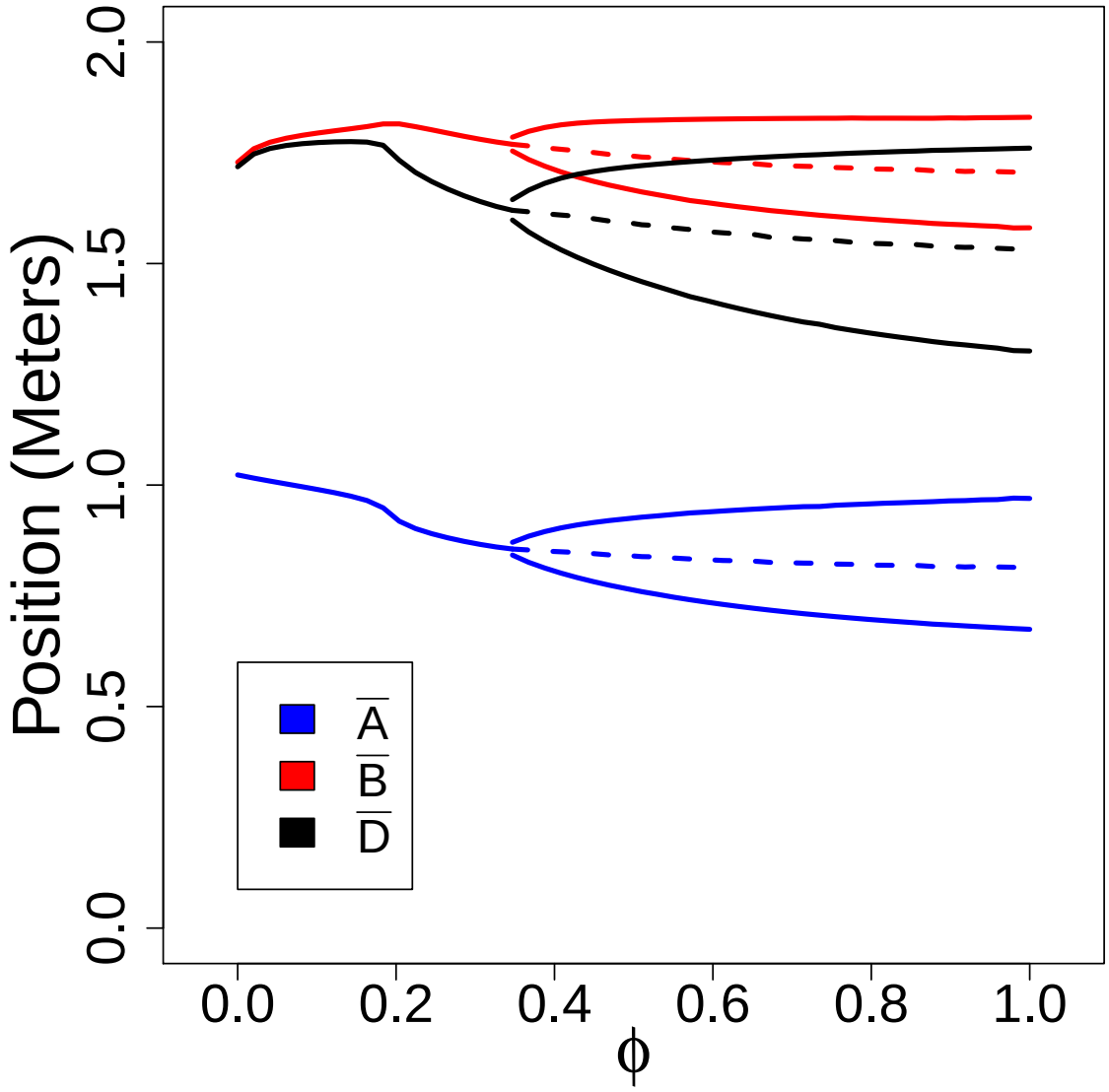

Figure 2.7. Bifurcation diagram of battle position and stability as a function of the parameter ϕ, with a Hopf bifurcation shifting from a stable equilibrium to an unstable equilibrium with stable oscillation at $\phi = 0.347$. We show mean, maximum, and minimum locations for the center of mass for each colony's searching ants and for dyads.

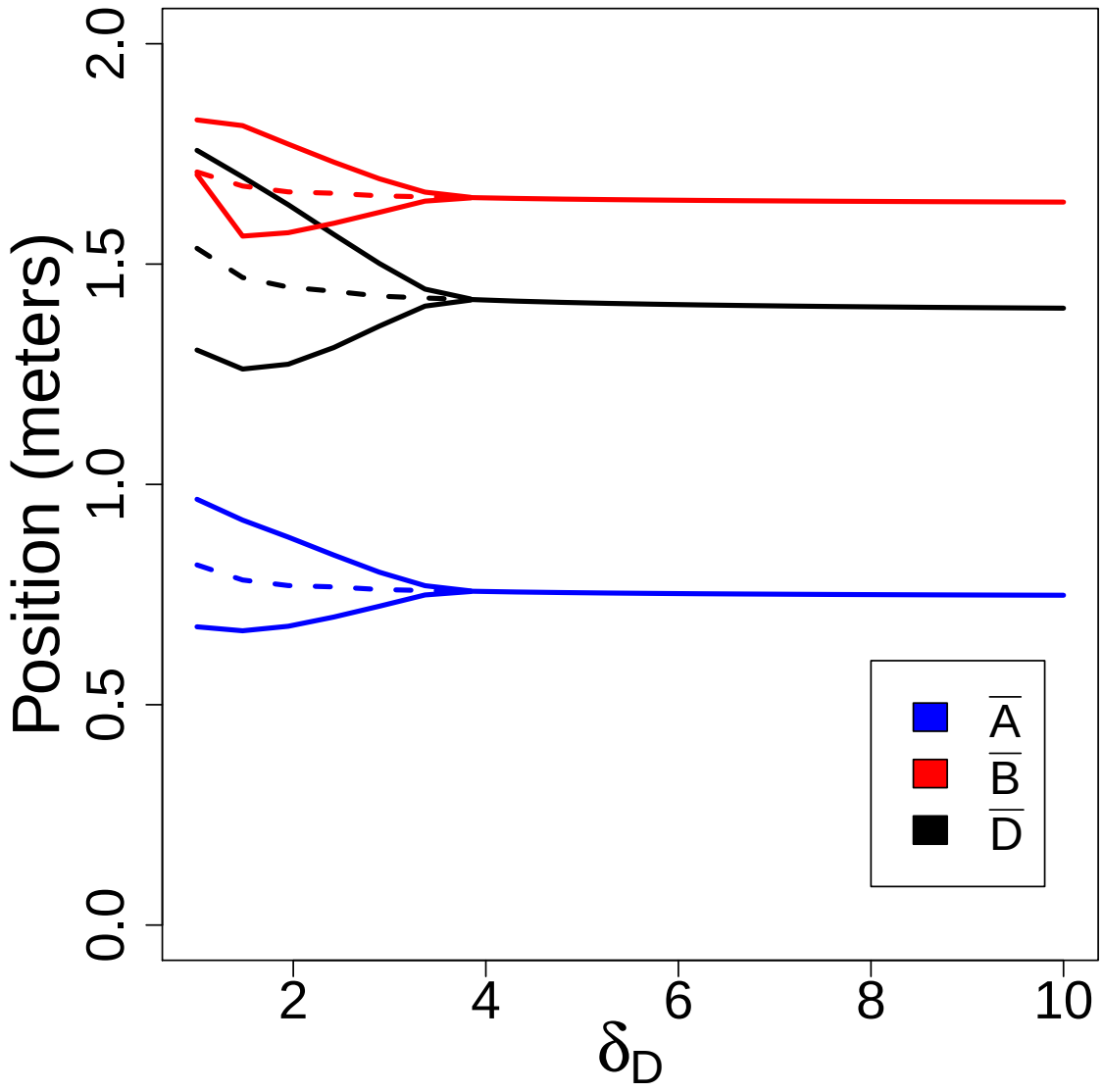

Figure 2.8. Bifurcation diagram of battle position and stability as a function of the parameter δ_D, with a Hopf bifurcation shifting from an unstable equilibrium with stable oscillation to a stable equilibrium at $\delta_D = 3.84$. We show mean, maximum, and minimum locations for the center of mass for each colony's searching ants and for dyads.

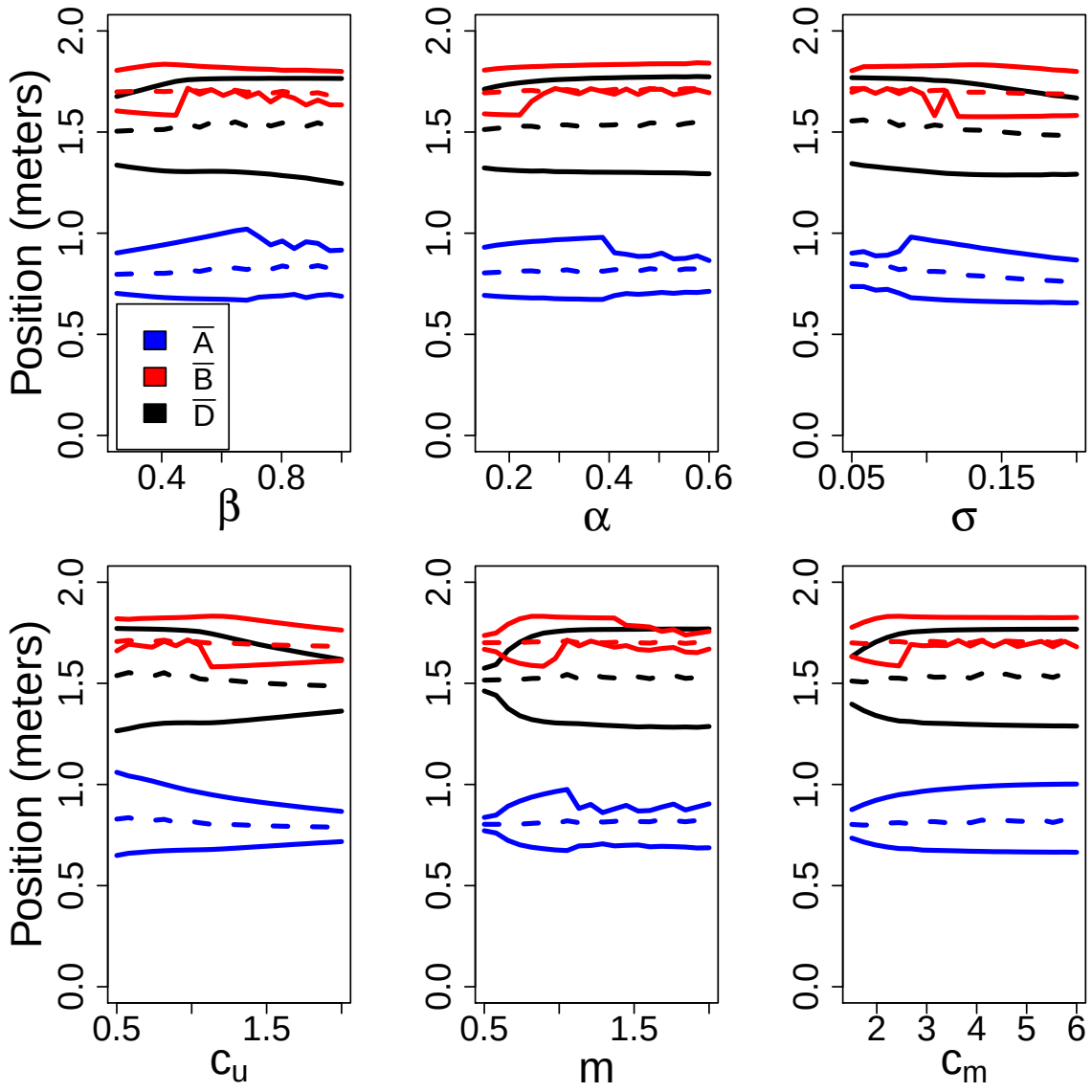

Figure 2.9. Changes in magnitude of oscillations of location of center of mass of dyads due to changes in parameter values. We show mean, maximum, and minimum locations for the center of mass for each colony's searching ants and for dyads.

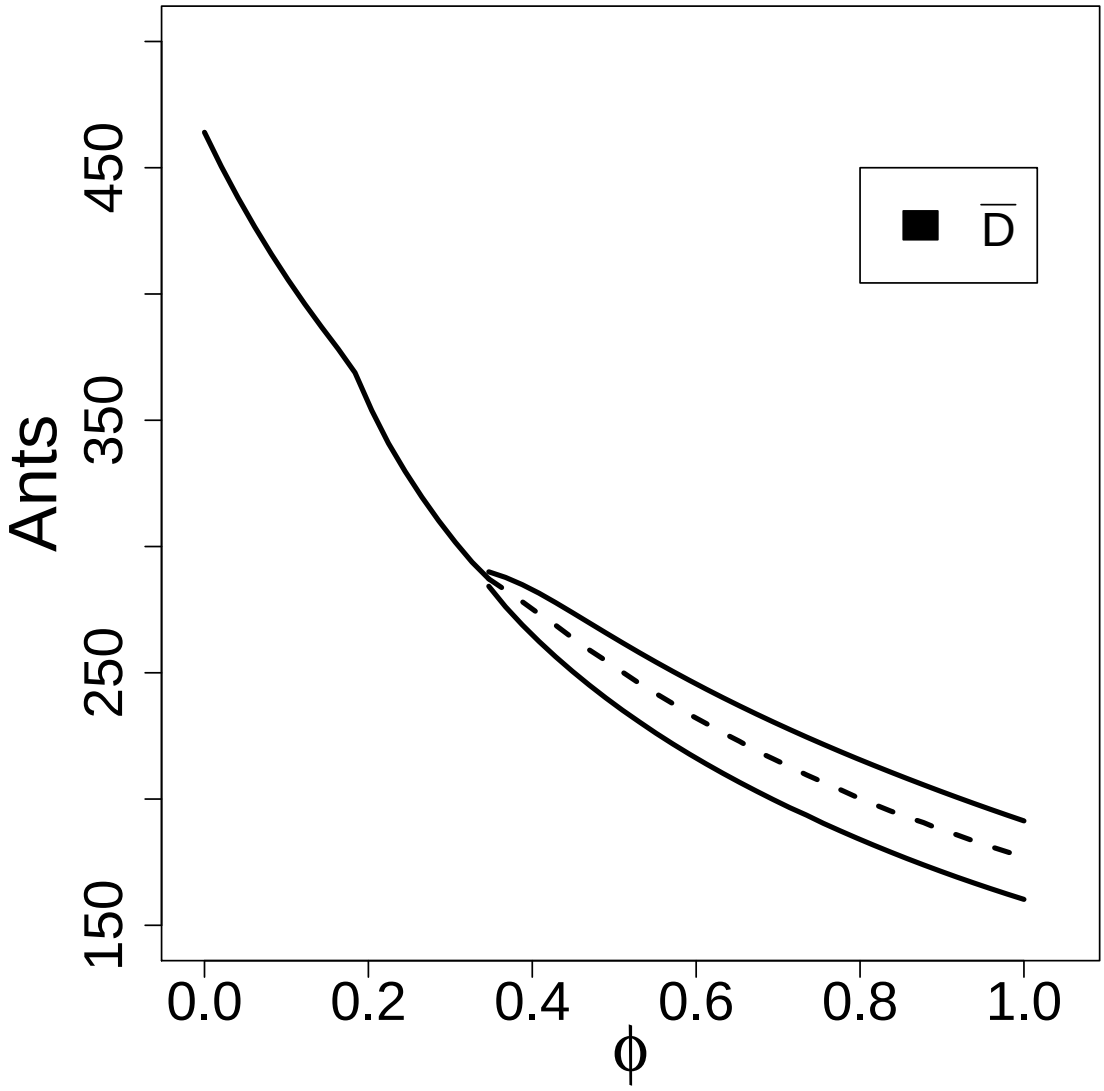

Figure 2.10. Bifurcation diagram of total ants in dyads and stability as a function of the parameter ϕ, with a Hopf bifurcation shifting from a stable equilibrium to an unstable equilibrium with stable oscillation at $\phi = 0.347$. We show mean, maximum, and minimum locations for the center of mass for each colony's searching ants and for dyads.

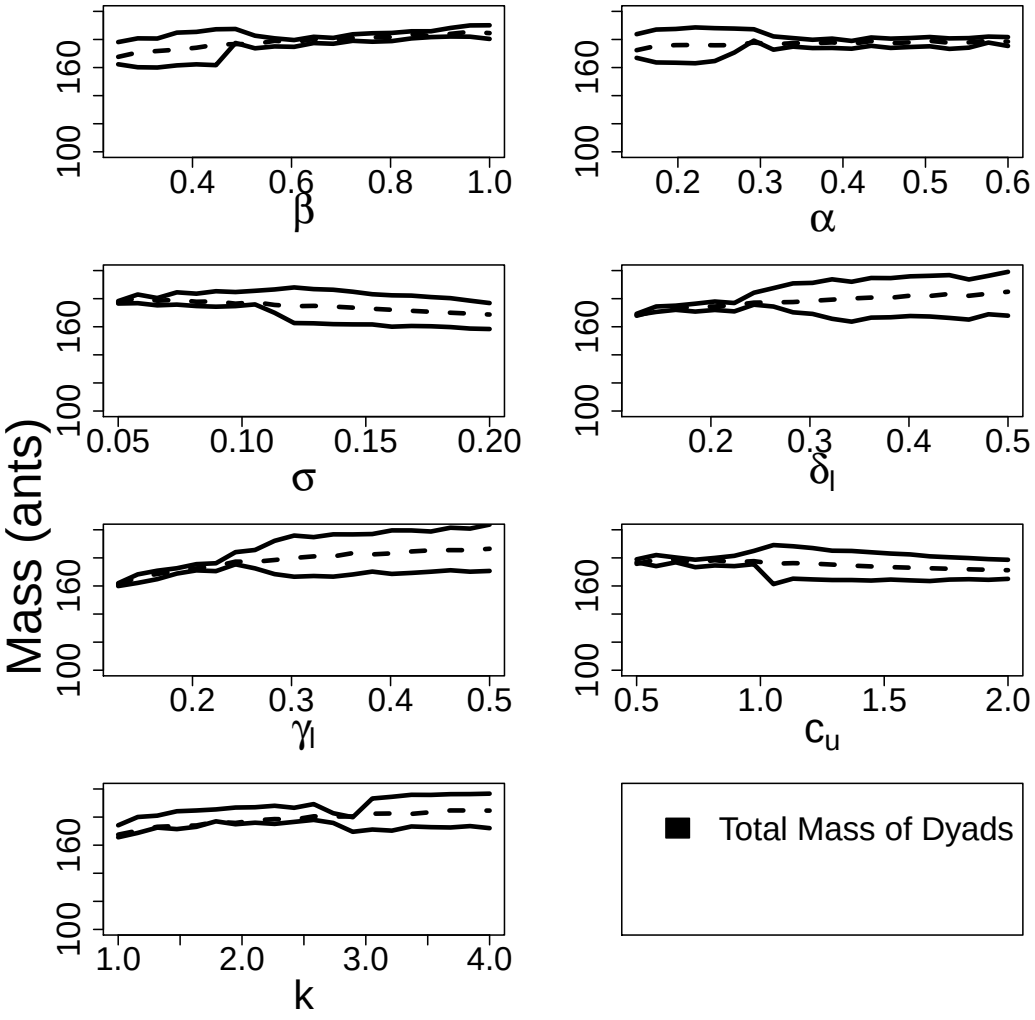

Figure 2.11. Changes in magnitude of oscillations of total ants in dyads due to changes in parameter values. We show mean, maximum, and minimum locations for dyads.

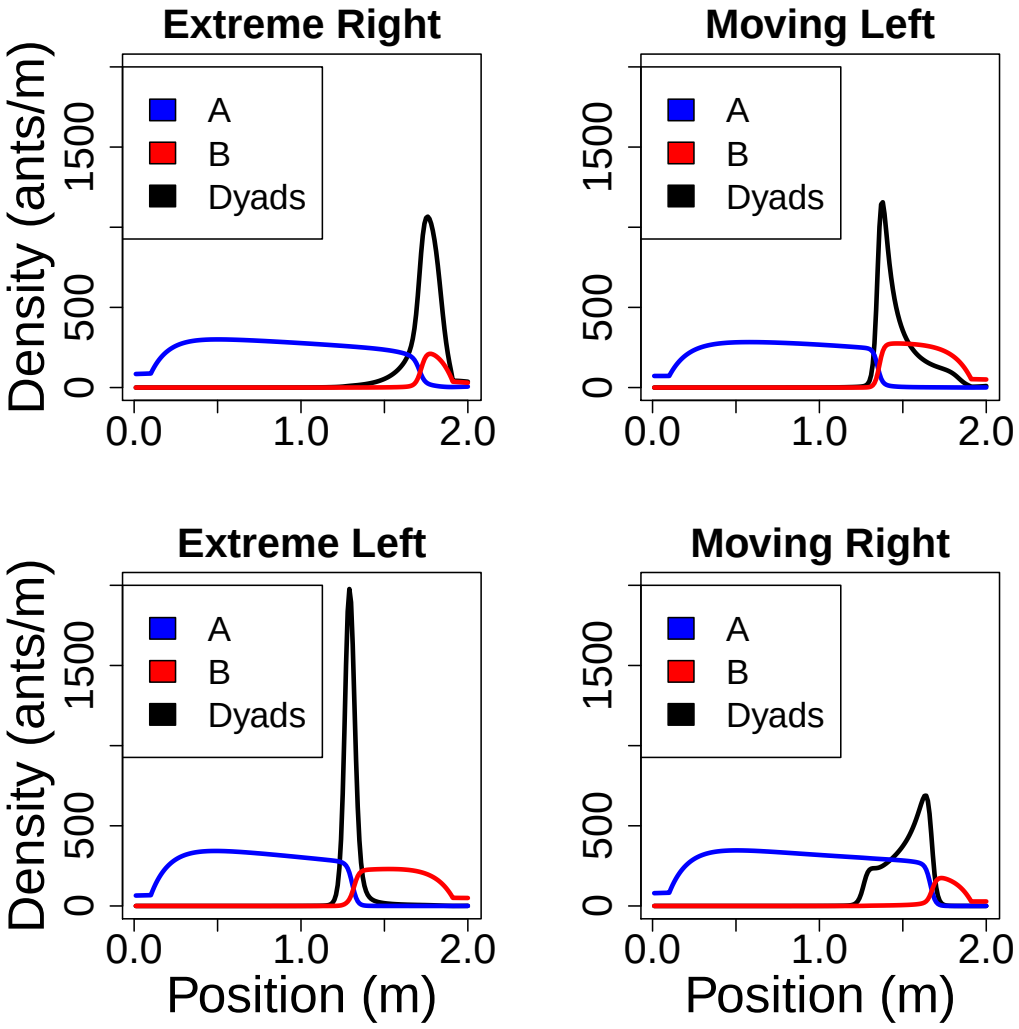

Figure 2.12. Sequential figures showing total dyads, searching ants from colony A, and searching ants from colony B as you move from left to right along the top and then left to right along the bottom. In the top left figure, the battle is at the extreme right of oscillations and the fewest ants are in the battle. The top right figure shows the battle at the midpoint moving from right to left while total ants in dyads begins to increase. The bottom left figure shows the battle at the extreme left position with a high peak in the total number of ants in the battle. The bottom right figure shows the midpoint of the battle moving from left to right. Colony A at $x = 0$ has 1000 ants and colony B at $x = 2$ has 500 ants.

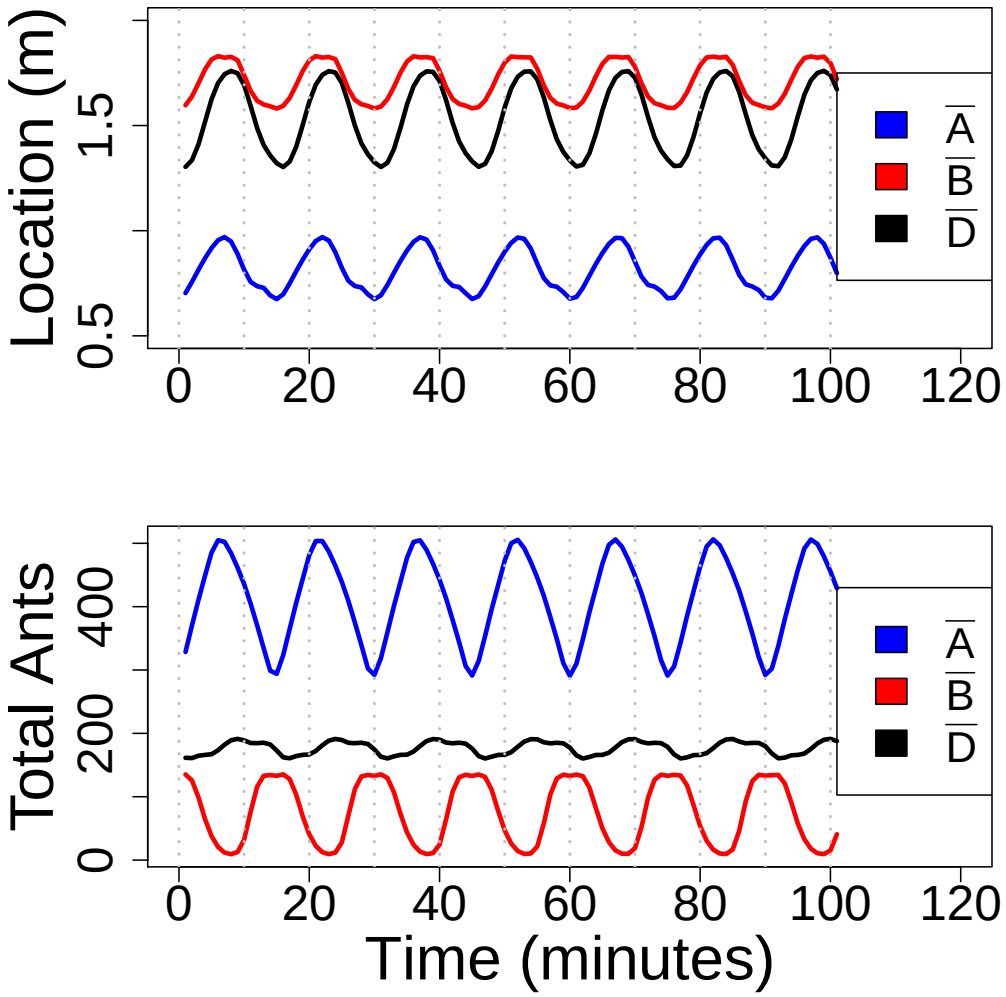

Figure 2.13. Oscillations in the battle position and total ants for $\phi = 1$. The locations of the center of mass of the searchers and dyads are in sync (top figure), but the total ants for the searchers from colony A and dyads are out of sync with total searchers from colony B by 180°. Colony A at $x = 0$ has 1000 ants and colony B at $x = 2$ has 500 ants.

CHAPTER 3

THE EFFECTS OF INITIAL CONDITIONS AND WORKER RULES ON BATTLE INITIATION

We use an agent-based model to test what conditions will make battle initiation favorable for intraspecific conflicts among ants. Ants of the genus *Tetramorium* were used to motivate the model because of their interesting territorial behavior. Simulations were run using different parameter values and initial conditions to determine how they affect the probability of a battle beginning. We find that battle initiation is most probable when initial conditions include several ants from each colony. Recruitment response to encounters with non-nestmate ants also influenced likelihood of having a battle. It is possible that battle initiation requires a stimulus outside of normal behavioral rules for ants.

3.1 Introduction

Territoriality exists in many ant species across the globe. Many of these ants will defend their territory at the boundaries and exclude most or all other species of ants from that territory [1, 25, 27]. Other species may not always patrol boundaries at all times, but rather respond either when encountering a non-nestmate in their territory or some outside stimulus such as a new or existing food source [8, 24]. Recruitment becomes necessary for this type of defense.

Ants of the genus *Tetramorium* recruit nestmates in two different ways, mass or group recruitment, to a particular location of interest for the nest [16]. In group recruitment, leaders assemble a group inside the nest that they then lead to the food source. To perform mass recruitment workers recruiting in the nest will excite workers in the nest to leave and follow pheromone trails to the location of interest.

Workers in ant colonies are able to make a variety of decisions based off of several different stimuli. For example, ants can make decisions based on quality of food source [16], quality of a new nest site [53], and territorial conflict [27]. Ants will make decisions

based off of encounters with nest and non-nestmates. Prior contact with more nestmates than non-nestmates will lead to more aggressive behavior when workers have to make a decision about fighting intruders in their territory [28]. Ants have been shown to count their steps [56] and identify nest and non-nestmates through contact, using pheromones and colony odor [26].

Stochastic modeling has been used for ants [31, 45]. In particular, Martelloni et al. in 2005 [34] used the diffusion-limited Gillespie algorithm to model two species of ants fighting in an arena with a radius of 5 cm. This was a spatial agent-based model with a discrete lattice of 1 cm by 1 cm cells. Ants will notice each other if they are in the same cell at the same time. This effectively gives them a 1 cm perceptual radius.

This paper investigates the initiation of intraspecific battles in two spatial dimensions between two colonies of ants. When ants are fighting, they form grappling pairs of ants (dyads) in the battle. The model investigates how battles start using an agent-based model that discretizes time but is continuous in space. Workers will make decisions based on how many ants contact dyads in the battle.

3.2 Methods

An agent-based model was created for two colonies of ants to allow the investigation of battle formation when workers from both colonies encounter each other. All simulations and processing of data were done using R 3.3.1 [46]. Once workers encounter each other, they can form a dyad during which each ant is collecting information that it then uses to make decisions. Upon leaving dyads, workers have three possible decisions: return to the nest as a leader to recruit nestmates to join the battle, become a searching worker in the battle, or become unmotivated and return to the nest to wait for recruitment. While in the nest, leaders recruit based on the rate ρ, lose motivation based on the rate δ_l, or return to the battle based on the rate γ_l. All parameter values used in simulations can be found in Table 3.1. Leaders return to the location of their last dyad and recruited ants go to the last dyad location of their leader. All states of ants can be found in Table 3.2.

The three decisions made as dyads break up are modeled with equations 3.1, which are the motivation equations from Chapter 2. The parameter k is a scaling factor for behavior of ants leaving dyads, m is the shape parameter of a hill function, and c_m and c_u are the

relative propensities to be unmotivated and motivated, respectively, with values shown in Table 3.2.

$$\begin{aligned} F_u(r) &= \frac{c_u k^m}{k^m + r^m + c_m r^m + c_u k^m} \\ F_s(r) &= \frac{k^m + r^m}{k^m + r^m + c_m r^m + c_u k^m} \\ F_m(r) &= \frac{c_m r^m}{k^m + r^m + c_m r^m + c_u k^m} \end{aligned} \tag{3.1}$$

The ratio of non-nestmate interactions with nestmate interactions during time in the dyad is given by r (equations 3.2), where a_{si} and b_{si} are all searchers, from colonies A and B respectively, within 1 cm of the dyad in time step i and T is the duration of the dyad. Any searching ant within a 1 cm radius of a dyad's location is counted as making contact with it. In order to keep r from being undefined in the event that no ants make contact with the dyad, we added 1 to the number of non-nest and nestmate encounters. Thus $r = 1$ if no encounters occur during the dyad.

$$\begin{aligned} r_a &= \frac{\sum_i^T (b_{si}) + 1}{\sum_i^T (a_{si}) + 1} \\ r_b &= \frac{\sum_i^T (a_{si}) + 1}{\sum_i^T (b_{si}) + 1} \end{aligned} \tag{3.2}$$

The functions give the probability of different decisions by ants leaving dyads where, $F_m(r)$ gives the probability of being motivated, where $F_s(r)$ gives the probability of becoming a searching worker, and $F_u(r)$ gives the probability of becoming unmotivated (Figure 3.1).

We started simulations with a small number of ants to investigate the probability of escalation to a full battle. To avoid waiting long times for an encounter between workers outside the nests to start battles, simulations were begun with all workers in dyads. If our initial numbers have fewer workers from one colony than the other, the number of dyads would be the number from the colony with the fewest initial ants. Additional workers from the other colony would start as searchers. We started simulations with 1 ant versus 1 ant, 10 ants versus 1 ant, 10 ants versus 4 ants, and 10 ants versus 10 ants from each colony. Positions for dyads and searching ants were found by selecting x and y coordinates from a normal distribution with mean of 150 and standard deviation of 50, except simulations investigating the effect of battle area size on battle initiation for which the mean for the y coordinate was 0.

A battle was determined to have started if total workers from each colony in the battle, except unmotivated workers, exceeded 14 workers. A battle was determined to have died out without starting if all workers from one colony are either nest or unmotivated workers. We stopped simulations at 2 hours if no battle began because ants run the risk of

desiccation if outside the nest for too long [15]. Our minimum threshold and time limits for determining whether or not an event occurs in an agent-based model are similar to the way influenza outbreaks are modeled by Merler et al. in 2013 [39].

To speed simulations up, we used an accelerated Gillespie algorithm with methods similar to the diffusion-limited Gillespie algorithm described in [34], except space is continuous, ants only form grappling pairs, and the battle area is much larger. The slowest process was waiting for ants to encounter each other when there were only a few ants searching in the battle area. We ran simulations to find an empirical time to encounter distribution for two searching ants based on their initial distance apart. The corresponding time it took for encounters was also determined in the empirical distribution. Any time there were only searching ants in the battle, the algorithm would sample from the empirical distribution for each pair of ants from different colonies, based on the distance between ants. The encounter with the shortest time was selected as the next encounter. This time was added to a cumulative time and if it exceeded 2 hours, then the battle was considered to have died out without starting.

A sensitivity analysis was performed on five parameters in the agent-based model: the rate of recruitment (ρ), the rate at which leaders in the nest lose motivation (δ_l), the rate at which leaders leave the nest to re-join the battle (γ_l), the probability of dyads forming (α), the rate at which dyads break up (δ_D), and the size of the battle area, which I will refer to as the elliptical battle. Data from the α, δ_l, γ_l, δ_D and area simulations were fit using linear regression.

Each colony has a soft reflecting boundary at 500 cm radius from the nest where ants turn back toward the nest with greater tendency the farther they get past the 500 cm radius. Inside the 500 cm radius, worker direction is modeled using a correlated random walk. New directions were chosen by taking the product of π with a random number sampled from a normal distribution with mean of 0 and a standard deviation of $\sqrt{\sigma}$. This new angle was then added to the current angle to giving a new direction. For most of the simulations, one colony was at the origin $(0,0)$ and the other was at the coordinate $(300,300)$. The elliptical battle simulation was changed by deforming the circular radius about each nest into an ellipse with the major axis toward the other nest and the minor axis perpendicular to a straight line drawn between the nests with the width given by b (equations 3.3). For

elliptical battle simulations, it was simpler to model one nest at the origin again, but place the other nest at $(424.26, 0)$ to keep the same distance between the nests as when the second nest was at $(300, 300)$. Data were fit using a linear regression.

$$\begin{aligned} \text{Elliptical Equation for Colony at Origin:} & \\ \left(\tfrac{x}{500}\right)^2 + \left(\tfrac{y}{b}\right)^2 &= 1 \\ \text{Elliptical Equation for Colony at (424.26,0):} & \\ \left(\tfrac{x-424.26}{500}\right)^2 + \left(\tfrac{y}{b}\right)^2 &= 1 \end{aligned} \tag{3.3}$$

Probabilities for a battle beginning were determined by running the simulation for at most 300 trials for each parameter value and initial condition, and dividing the successes by the total number of trials. This is similar to how probabilities were found by Hotchkiss et al. in 2005 [29]. To increase speed of simulations, a function for the error (equation 3.4) was checked after each increment of 100 trials to see if it was less than 0.005. The error function we used is the standard error divided by the probability found thus far to make it like the coefficient of variation and provide a more stringent requirement. To keep E from being undefined, 10^{-16} was added to the denominator, where p is the probability of a battle beginning as determined by taking the quotient of the number of successes and trials (N). If the error met this threshold ($E \leq 0.005$), simulations were halted.

$$E = \sqrt{\frac{1-p}{pN+10^{-16}}} \tag{3.4}$$

Only in a few of the 10 versus 10 cases the probability of a battle beginning was large enough that simulations were halted. All halted simulations ran for 100 trials and no simulations were halted after 200 trials.

In the simulations testing recruitment rate, a limiting probability ($\rho \to \infty$) was calculated using equation 3.5. The probability of a battle is P_B and n_a and n_b are the number of ants from each colony in the battle at the beginning. The motivation function from equations 3.1 is $F_m(1)$ and is evaluated at 1 since there aren't any searching ants in the battle area in the 1 versus 1 and 10 versus 10 cases. Searchers contacting dyads are unlikely in the 10 versus 1 and 10 versus 4 cases so $r = 1$ is also used in those two cases.

$$P_B(n_a, n_b) = \left(1 - (1 - F_m(1))^{n_a}\right)\left(1 - (1 - F_m(1))^{n_b}\right) \tag{3.5}$$

3.3 Results

The initial number of ants in the battle from each colony most strongly influences the probability of a battle starting. In all simulations, the maximum probability of a battle beginning for the 1 versus 1 case is less than 0.15. In the 10 versus 10 case, the probability of a battle is near 1 for baseline parameter values. The most variability in probability of a battle beginning occurs in the 10 versus 4 initial condition, followed by the 10 versus 1 initial condition.

The recruitment rate, ρ, has the largest effect on the start of battles. For all four initial conditions the probability of battle increased with an increase in recruitment rate (Figure 3.2). Dashed lines represent the limiting probability as ($\rho \rightarrow \infty$) and are given by equation 3.5. The 10 versus 4 initial condition can exceed the limiting probability for two reasons: Ants from the smaller initial condition might experience $r > 1$ and have a higher probability of being motivated. Some of the ants leaving dyads may become searching ants instead of unmotivated ants and since there are up to 4 searching ants available, it was much more likely that another encounter would occur in a short enough time that the battle could still begin.

Probability of a dyad forming, α, has a positive association with the probability of a battle beginning (Figure 3.3) because all information and decision making is done in a dyad, so the only way an ant can become motivated and return to the nest to recruit is by forming a dyad.

The parameters δ_l and γ_l, which represent the rate at which leaders become nest ants or return to the battle, have a negative correlation with the probability of a battle beginning (Figure 3.4 and Figure 3.5). Increasing either of these two parameters reduces the number of recruits, which also reduces the probability of a battle beginning.

Battle formation was only weakly negatively associated with the width of elliptical battles, b (Figure 3.6). Because both leaders and recruits return to the location of previous encounters, relatively few go all the way to the boundary and still return to the battle as the width is increased. In the case of 1 versus 1, the linear regression has a positive slope, but it is not significant. The dyad break up rate, δ_D, does not appear to have any measurable effect on the start of battles (Figure 3.7).

3.4 Discussion

Ant battles begin when a small number of ants from different colonies encounter each other and then recruit sufficient new ants to escalate the conflict. We investigated how the parameters of an agent-based model of recruitment affect the probability that a battle will indeed begin, finding that parameters controlling recruitment are indeed most important. In particular, higher recruitment rate (larger value of ρ) or longer recruitment duration (lower δ_l or γ_l) led to increased chance of battle initiation. Recruitment has this strong effect because we define battle initiation as recruitment of 15 or more workers from each colony. The negative correlation with δ_l and γ_l occurs because an increase in each of these rates causes leader ants to spend less time recruiting. The parameter α controls the probability of dyad formation with larger values associated with higher probabilities of battle initiation because more ants forming dyads leads to more motivated ants and leaders in the nest, and subsequent recruitment. A larger battle area reduces the probability of battle initiation because ants are less likely to encounter each other, leading to fewer numbers of motivated ants returning to the nest to recruit. There will also be fewer contacts by searching ants with dyads, leading to less of a chance for ants to become motivated. The duration of dyads, determined by δ_D, has no effect on the probability of battle initiation because it alters the timing, but not the extent of recruitment.

Due to the role of recruitment, Figure 3.2 becomes the key to understanding the beginning of battles. In the limiting case where $\rho \to \infty$, it takes only one ant from each colony leaving a dyad motivated because each will effectively recruit their entire colony. The probability of battle initiation can exceed the theoretical limit (dashed lines in Figure 3.2). However in the 10 versus 4 case, ants from the colony with fewer initial ants could be more highly motivated than indicated in equation 3.5 due to encounters with searching ants from the more numerous colony. In addition, some ants will leave dyads as searching ants and may encounter a non-nestmate within the 2 hour time limit and possibly become motivated themselves.

Initial numbers of ants have the largest effect on the probability of battles starting. This would indicate that some outside stimulus may be necessary for battle formation in ants. In his research on pavement ant battles in 1879, McCook [37] observed one battle that had some kind of fatty matter at the center of the battle. Baits have been used to initiate

battles by getting workers to recruit to the edges of their territory and then moving the baits close enough together to allow workers to encounter each other [41]. Other than during initiation of battles using baits, the beginning of pavement ant battles have not been observed and we do not know whether a stimulus is actually responsible for battle initiation.

Alternatively, ants that have had more nestmate interaction than non-nestmate interaction are more aggressive and likely to form dyads [28], which could translate into a higher likelihood that initial ants in dyads would become motivated. Unfortunately, there is no information available on the probability of recruitment based on this stimulus.

Battle initiation depends on initial conditions and the recruitment response of workers leaving dyads. Any parameter that strengthens the recruitment response will increase the probability of battle initiation. While our results suggest that it may require an outside stimulus to initiate a battle, it is unclear what form such a stimulus might take.

Table 3.1. Parameters in the individual-based model.

Parameter	Description	Value or Range
	Parameters Describing the Nest	
δ_l	Rate at which leaders become unmotivated	$0.25/60$ sec^{-1}
γ_l	Rate at which leaders leave the nest	$0.25/60$ sec^{-1}
ρ	Recruitable ants leave for the battle	$0.02/60$ sec^{-1} ant^{-1}
	Parameters Describing Battle	
V	Speed of ants	1 cm/sec
σ	Searcher switching rate	0.2 sec^{-1}
δ_D	Rate at which dyads break up	$1/60$ sec^{-1}
α	Probability of dyad from encounter	0.2
	Parameters in the $F(r)$ equations	
k	Scaling factor in functions for post-dyadic behavior	2.0
m	Shape parameter for post-dyadic behavior	1-3 (1)
c_u	Relative propensity to leave dyad unmotivated	1.0-3.0 (1.0)
c_m	Relative propensity to leave dyad motivated	1.0-3.0 (3.0)

Table 3.2. States for ants in the model.

State	Description
Nest Ants	
Recruitable	Ants available to be recruited to the battle
Leaders	Ants recruiting nestmates
Battle Ants	
Traveling	Recruits and leaders returning to leader's last dyad location
Searching	Ants searching the battle area using a correlated random walk
Dyads	Ants in a grappling pair
Motivated	Ants returning to the nest to become leaders
Unmotivated	Ants returning to the nest to become recruitable

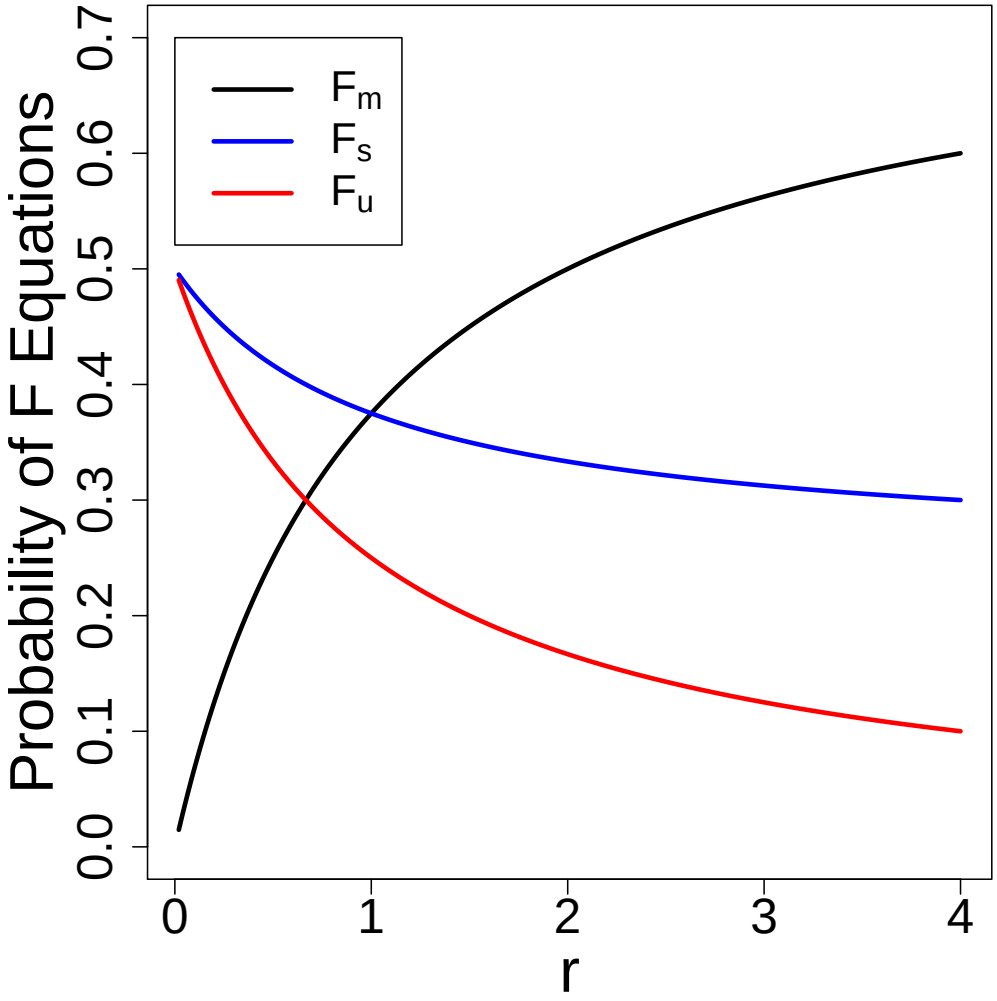

Figure 3.1. Plot of motivation functions $F_m(r)$, $F_s(r)$, and $F_u(r)$. Parameter values are $k = 2$, $m = 1$, $c_u = 1$, and $c_m = 3$.

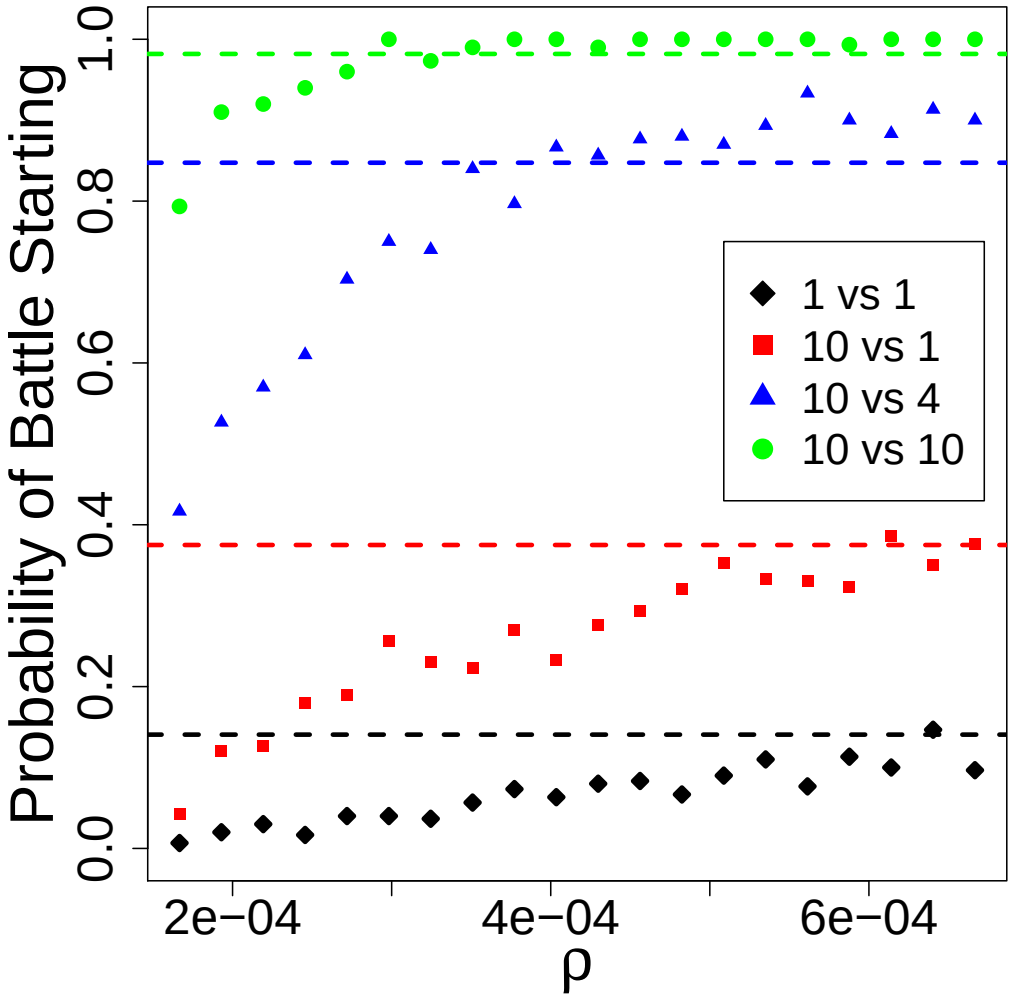

Figure 3.2. Probability of a battle beginning for a range of recruitment rate values (ρ) and four initial conditions for the battle. Dashed lines represent the limiting probability as determined by equation 3.5 ($\rho \to \infty$).

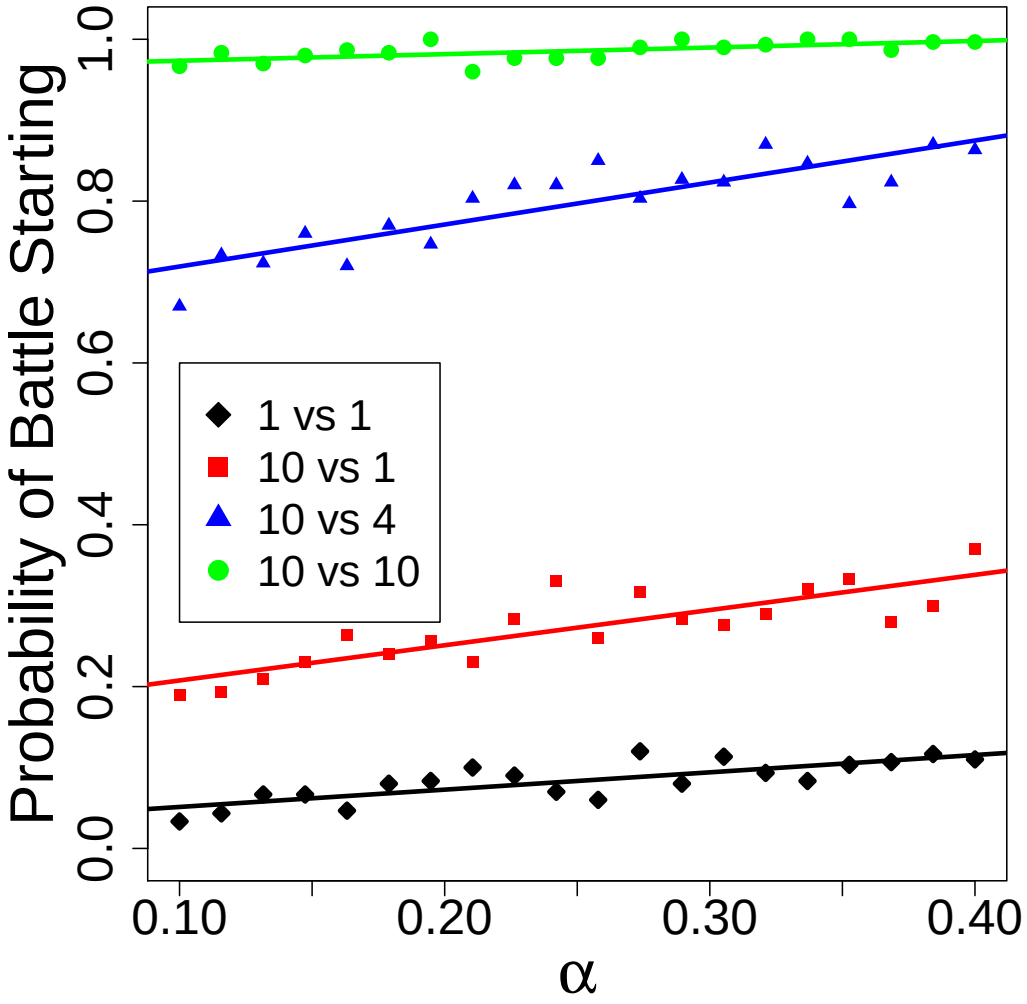

Figure 3.3. Probability of the battle beginning with a range of values for the probability of a dyad forming (α). Linear regressions have r^2 values of 0.623, 0.710, 0.746, and 0.407 for the 1 vs. 1, 10 vs. 1, 10 vs. 4, and 10 vs. 10 cases, respectively.

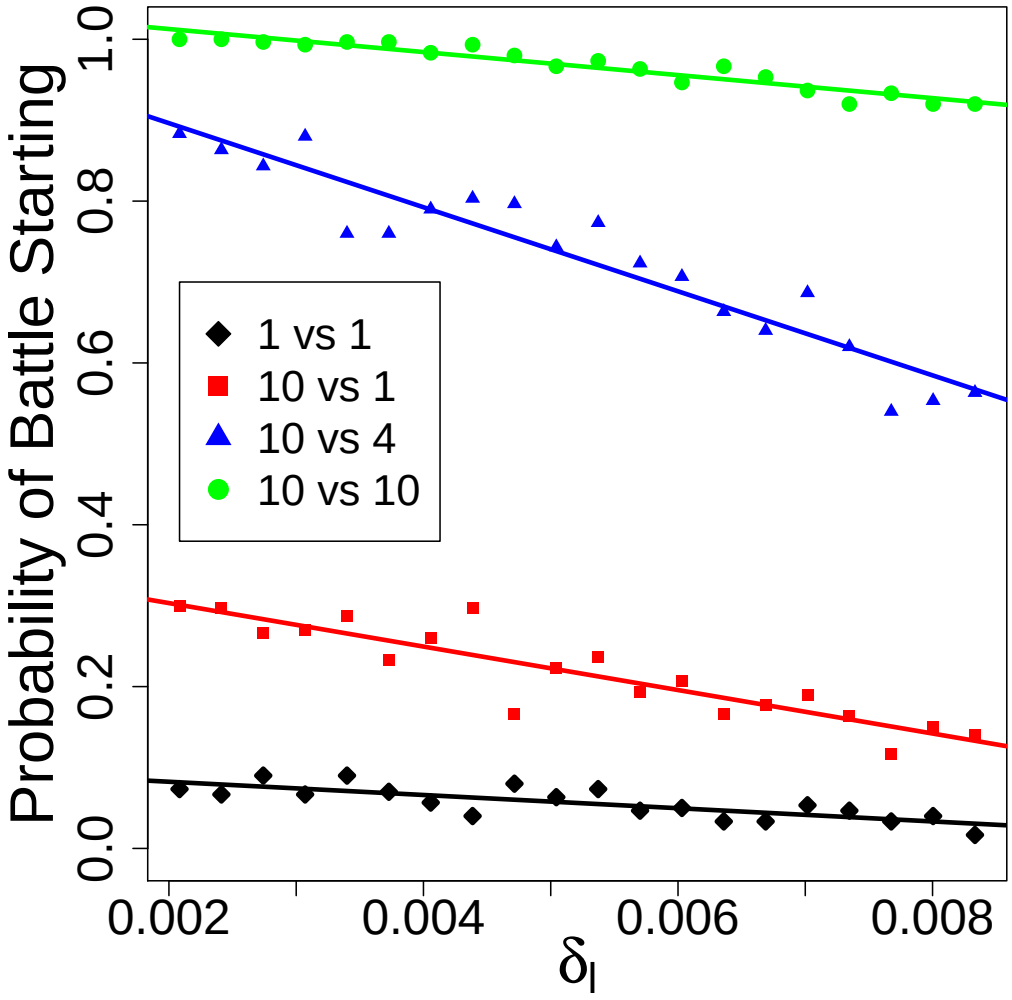

Figure 3.4. Probability of the battle beginning with a range of values for the rate at which leaders lose motivation (δ_l). Linear regressions have r^2 values of 0.618, 0.815, 0.899, and 0.912 for the 1 vs. 1, 10 vs. 1, 10 vs. 4, and 10 vs. 10 cases, respectively.

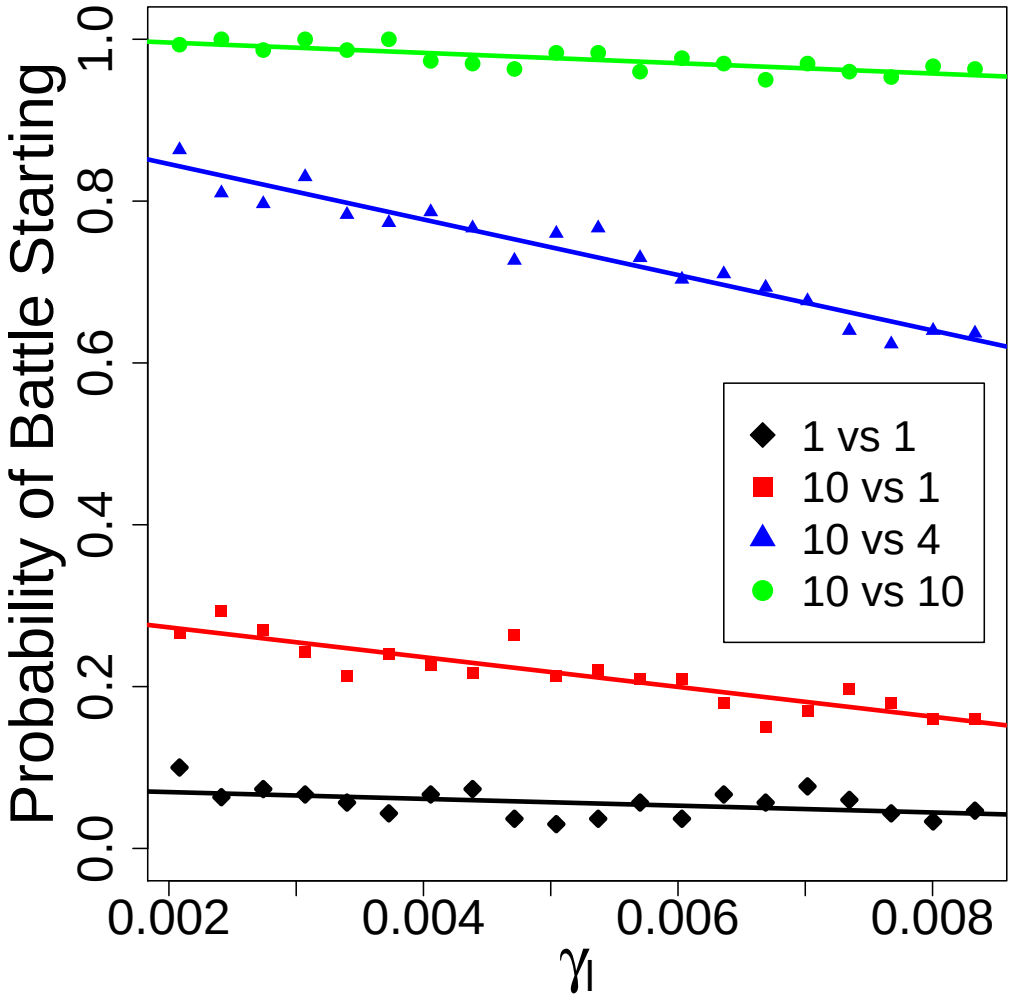

Figure 3.5. Probability of the battle beginning with a range of values for the rate at which leaders leave the nest to re-enter battles (γ_l). Linear regressions have r^2 values of 0.208, 0.789, 0.929, and 0.638 for the 1 vs. 1, 10 vs. 1, 10 vs. 4, and 10 vs. 10 cases, respectively.

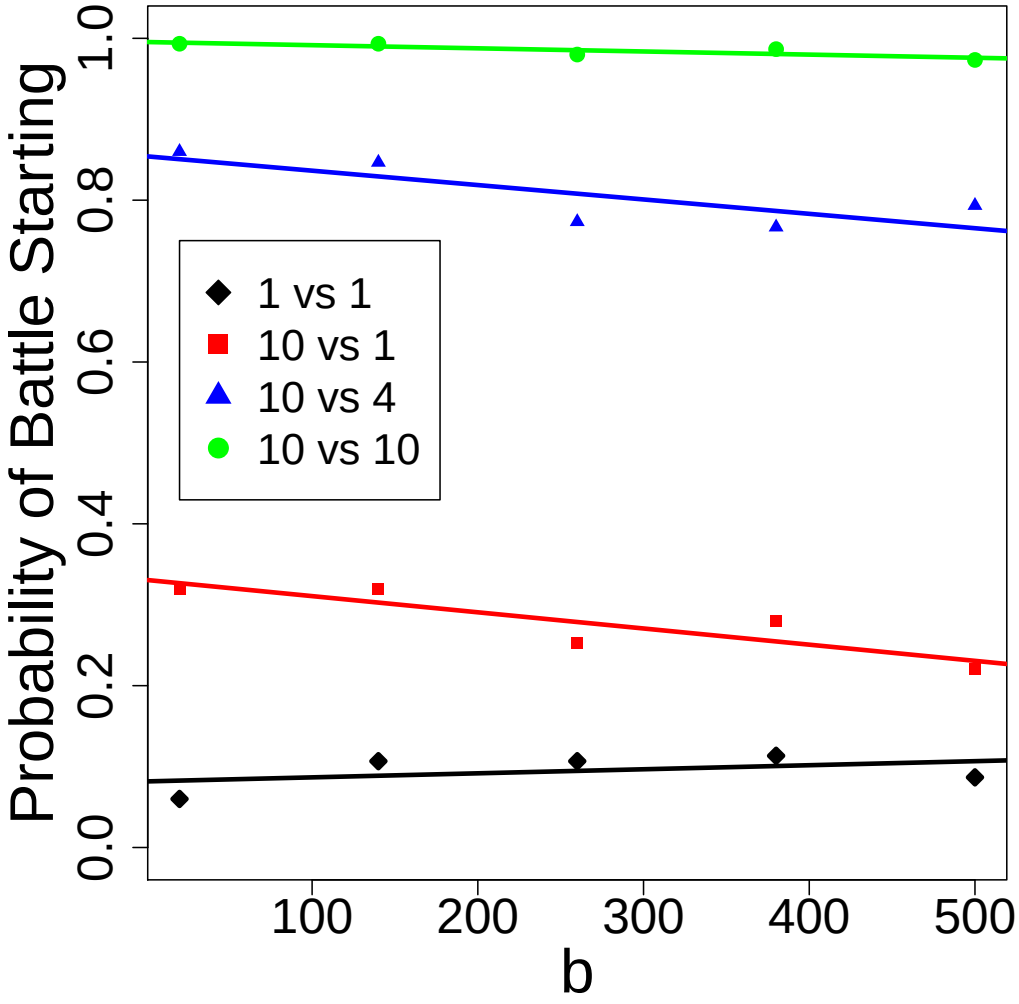

Figure 3.6. Probability of battles beginning with a range of values for b (equation 3.3), the minor axis in the ellipse controlling the soft reflecting boundary. Linear regressions have r^2 values of 0.189, 0.768, 0.621, and 0.721 with corresponding p-values of 0.4641, 0.051291, 0.1132, and 0.0689 for the 1 vs. 1, 10 vs. 1, 10 vs. 4, and 10 vs. 10 cases, respectively.

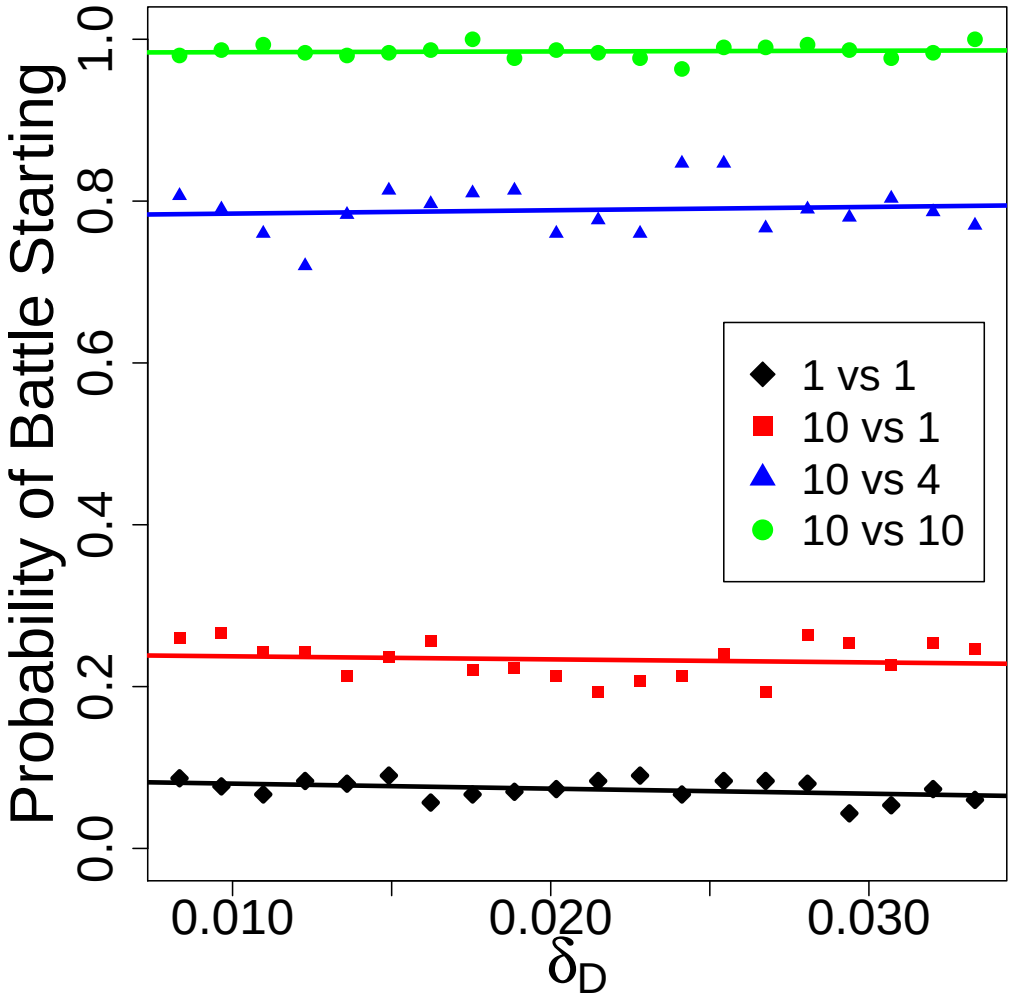

Figure 3.7. Probability of the battle beginning with a range of values for the rate at which dyads break up (δ_D). Linear regressions have r^2 values of 0.142, 0.016, 0.011, and 0.007 for the 1 vs. 1, 10 vs. 1, 10 vs. 4, and 10 vs. 10 cases, respectively.

CHAPTER 4

WORKER RULES AND COMMUNITY STRUCTURE

We extend a model for territoriality between two colonies to determine a distribution of territory sizes for a one-dimensional community. Demographic effects of the community are coupled with territory sizes in the community to model founding, growth, and death of colonies. We find that the lifespan of colonies and year-to-year worker survivorship most affect how many ants are supported by the community. The worker rules controlling recruitment and how workers assess battles had large effects on diversity of colonies and total number of colonies in the community.

4.1 Introduction

Most ant species display some form of territoriality, whether defending actual space, nests and brood, or food sources [27]. Some species have absolute territories that are consistently patrolled by workers and defended against any non-nest ants [1], while others defend food sources instead of absolute territories [24]. For absolute territories, new colonies nearby pose a threat to an existing colony, leading to killing of founding queens (Figure 4.1). Due to this danger, many queens, including those of the genus *Tetramorim* found claustrally, will dig a nest and then seal it off until the first round of brood have matured and are able to perform tasks outside the nest [30]. The first workers from such colonies are often small (minims) and can easily escape notice. Newly established colonies of *Pogonomyrmex barbatus* focus on expanding territory in order to grow, while already established colonies focus on producing reproductive individuals [22]. This suggests that once colonies control enough territory, the intake of energy from the territory meets the colony's needs.

Mathematical models of territories often fall into two categories: (1) construction of a PDE from underlying movement behavior and (2) using a statistical physics approach

that analyzes individual movement and interactions without taking mean field continuum limits [44]. One issue with statistical methods is they lack predictive power [40]. Territorial behavior in wolves and their interactions with deer was modeled using a diffusion approach along with tracking scent marking, which described the establishment of buffer zones between wolf territories [33].

Models of ant territoriality have mainly fallen into two categories: economic models where territory and colony size reach some balance [1, 25], or the use of Lanchester's models of combat [20]. Two different modes of Lanchester's models are used to describe different styles of combat in ants. The square law focuses on colonies with many small workers that can combine their efforts in combat to defeat non-nestmate workers through recruitment. The linear law focuses on worker traits like size or weaponry (more lethal mandibles, or stings) allowing them to better fight other workers [4]. These models could be important for invasive species that often have large colonies with small workers and effective recruitment strategies [38].

Ants of the genus *Tetramorium* provide much of the motivation for the model created in this chapter. These ants are commonly called pavement ants due to their habit of nesting under and around paved surfaces like sidewalks and roadways. It has been observed for a long time that these ants stage large intraspecific battles during the spring and summer months [37, 47]. Battles may last between a few hours or several days and may serve as an information gathering technique for neighboring colonies to determine the division of territory. After battles, colonies establish buffer zones between territories that workers rarely enter [41]. These territorial battles determine community structure each year, allowing colonies to establish a territory for foraging and food collection.

We extend the modeling techniques from Chapter 2 but to track a community of colonies rather than just two colonies. The model includes establishment of new colonies, and the death of aging and new colonies that are unable to gain enough territory to grow. Hölldobler and Lumsden in 1980 [25] discuss economic models of territoriality where there are costs of defense, and benefits based on area of territory controlled by the colony. Overall profit of territories is given by the difference in benefits and costs. Boundaries occur where the costs and benefits balance, thus territories will be established that are economically defensible. Because energy intake by an ant colony can be modeled by

overall territory controlled, this provides a way to link a model of colony size based on its territory with the "battle model" from Chapter 2.

4.2 Methods

To create a community-based model, the battle model developed in Chapter 2 was extended to work with multiple colonies to calculate territory controlled by each colony. Colonies were placed along a 500 meter line simulating a sidewalk or other paved surface [36]. The battle model determines the territory size. In absolute territories, territory controlled is proportional to resources controlled because all workers searching the area come from that colony. The size of the territory controlled determines if a colony will increase in workers if it is large enough or decline in workers if a colony has outgrown its territory or loses territory to a neighboring or newly established colony.

Newly mated queens select nest sites uniformly from the region modeled. Each queen had a probability of surviving of 0.5. Queens that survive give rise to young colonies that start with a total of 25 workers to simulate the emergence of a colony from the claustral phase of colony development. Because colonies are arranged in one dimension, each has two neighbors, one on each side, except for those at each end, which have only one neighbor.

Because solving the battle model using the ReacTran package [51] in R 3.3.1 is time consuming, we developed interpolation functions to find territory sizes. The interpolation functions varied three input variables, two for the colony sizes of neighbors in the battle (25 workers to 1275 workers) and intercolony distance (0.02 meters to 5 meters). Two parameters were varied to investigate their effects on the community. Parameters varied were recruitment rate ρ and information parameter ϕ. The recruitment rate in the battle model controls how fast leader ants in the nest are able to get nestmates to enter the battle. The information parameter controls how information in the battle is collected; if $\phi = 0$, then only searching ants are collecting information in the battle and if $\phi = 1$, then only dyads are collecting information in the battle. Three values of recruitment were tested $\rho = 0.000667$, $\rho = 0.02$, and $\rho = 0.04$. Two values of information parameter were $\phi = 0$ where all information is gathered by searchers and $\phi = 1$ where all information is gathered by dyadic ants as in the battle model. Interpolation was done using the built-in loess

command in R 3.3.1 [46].

Colony growth or decline is modeled by equation (4.1) where N_i is the colony at the start of the year and N_{i+1} is the new colony size after territory size (T) is determined. The constant c is the overall growth per territory size and σ_D is the proportion of workers that survive from the previous year.

$$N_{i+1} = \sigma_D N_i + cT \tag{4.1}$$

Colonies that decline to fewer than 25 ants are considered to be too small to compete and are removed from the community (i.e., death). Colonies that do not meet a minimum territory size (0.1 meter) are also removed from the community. Each colony has a probability of death given by q during the transition from one year to the next. Thus, colonies are expected to live on average $\frac{1}{q}$ years. We conducted three experiments for each of the three recruitment rates. The first experiment tests the effects of the information parameter, and both values of the information parameter are used in the other two experiments. The second experiment investigated the effects of a longer colony lifespan by making the probability of death q smaller. The last experiment reduces worker survivorship. See Table 4.1 for complete parameter information. Simulations started with a random number of mature colonies in the community and then were allowed to run until the distribution of new and mature colonies stabilized. Data are collected from a 200 year simulation following stabilization.

Information tracked during simulations of the community model include worker number for each colony, colony location, territory size, and age of the colony. Total ants summed over all colonies were compared to the total theoretical maximum number of ants supported by the community. The total theoretical maximum was found by setting

$$A_{max} = \sigma_D A_{max} + cT_{com} \tag{4.2}$$

and solving for the total maximum ants supported, A_{max}, where T_{com} is the community size, c is the growth per territory size, and σ_D is the proportion of workers that survive to the next season.

$$A_{max} = \frac{cT_{com}}{1 - \sigma_D} \tag{4.3}$$

Colony richness (R), using the inverse Simpson diversity index [50] where p is the proportional abundance (equation 4.4), and total colony numbers were compared to the total ants

to find out whether the maximum number of ants in the community occurs when there are fewer large colonies or more small colonies. The year-to-year changes in colony sizes were also investigated to see whether colonies of different sizes tend to grow, stay the same, or shrink in size.

$$R = \frac{1}{\sum p^2} \tag{4.4}$$

4.3 Results

In simulations, both colony diversity and total ants vary through colony deaths and regrowth (Figure 4.2). The total theoretical maximum found for a community 500 meters long is 100,000 ants for $\sigma_D = 0.7$ and $c = 60$. When σ_D is reduced to 0.1 and c increased to 100, the theoretical maximum is 55,555 ants. The closest communities come to either theoretical maximum is when $\sigma_D = 0.1$, which corresponds to the maximum of 55,555 ants. When $q = \frac{1}{20}$, the community is closer to the maximum of 100,000 than when $q = \frac{1}{6}$.

To investigate how colonies change from year to year, each colony size was compared in consecutive years. Smaller colonies tend to increase while larger colonies tend to decrease (Figure 4.3) with $\sigma_D = 0.7$ and $q = \frac{1}{20}$, the trend of small colonies increasing and large colonies decreasing is small. With $\sigma_D = 0.1$ and $q = \frac{1}{6}$, the trend of small colonies increasing and large colonies decreasing is more pronounced (Figure 4.4). The variability of colony size from one year to the next is much larger when $\sigma_D = 0.1$ and $q = \frac{1}{6}$ than when $\sigma_D = 0.7$ and $q = \frac{1}{20}$. The observed high diversity could come from either change, because a larger value of q consistently opens space for smaller colonies to fill due to more colony deaths, while a smaller σ_D reduces the stability of larger colonies allowing more worker deaths that must be replaced by energy intake in the territory. Two main factors affect colony size the next year: the growth per territory size (c) and the survivorship (σ_D) of workers from equation (4.1). The effects of those parameters tend to balance each other out for medium sized colonies.

In order to determine whether diverse communities with more small colonies or less diverse communities with large colonies are closest to the theoretical maximum, total number of ants was plotted versus the diversity index. For each experiment, there was a slight increase in total ants with increasing diversity (Figure 4.5). While the figure shows only one of the experiments, this relationship is consistent with other parameter values.

Total numbers of ants remained consistent within each experiment, although total ants changed with different σ_D and c values. Because the theoretical maximum number of ants is given by equation (4.3), changes in the survivorship of workers (σ_D) and the per distance benefit of territory (c) change the theoretical maximum (Figure 4.6). The total number of colonies and the diversity index do depend on the information parameter ϕ and recruitment parameter ρ. For both experiments, $\phi = 0$ and $\rho = 0.000667$ had the largest number of colonies and were the most diverse (Figure 4.7). The smallest number of colonies and least diverse community occurs when $\phi = 1$ and $\rho = 0.04$ (Figure 4.8). The model predicts that the number of colonies is most sensitive to the recruitment rate and dyadic information collection when colony lifespan is longest with $q = \frac{1}{20}$. The number of colonies least sensitive to the recruitment and dyadic information parameters occurs when survivorship of workers is low ($\sigma_D = 0.1$). Changes in lifespan of the colony create the largest range in diversity, while low worker survivorship produces the smallest range in diversity.

4.4 Discussion

We used a model of territorial battles between pairs of colonies to predict the distribution of colony sizes in a community arranged along a one-dimensional habitat. The model combines individual behavior during battles with the demographic consequences of territory. We studied how key parameters from each aspect of the model affect the resulting community. In particular, we examined the recruitment parameter ρ, which controls how effectively new ants join the battle and the information parameter ϕ that controls which workers asses the state of the battle with $\phi = 0$ dependent on searchers and $\phi = 1$ on ants locked in dyads. At the colony level, we investigated the colony survival probability q and the individual worker survival σ_D.

We compare simulation results with the theoretical maximum total number of ants and colony diversity. Communities come closest to each theoretical maximum when colony survival is high and worker survival is low ($q = \frac{1}{20}$, $\sigma_D = 0.1$) and farthest when $q = \frac{1}{6}$ and $\sigma_D = 0.7$.

When recruitment is increased and information is collected by ants in dyads, overall diversity and total colony numbers decline, while maintaining consistent numbers of ants

overall, suggesting that there are fewer colonies overall of larger sizes. In this case, larger colonies have a competitive advantage through recruitment of more ants to the battle. Because larger colonies end up with more of the territory, spatial effects come into play for small colony survivorship. Large colonies have to recruit over longer distances, diluting the number of ants recruitment brings to the battle and allowing small colonies that are far enough away to survive. Large colonies tend to decline and small colonies tend to increase from year to year.

In her work on *Pogonomyrmex barbatus*, Gordon in 1995 [22] found that once colonies are established, they focus less on gaining territory and more on producing reproductive ants. This transition should be controlled by reaching a colony size that balances territory controlled and overall growth, as in the economic models in [25]. It would be interesting to investigate if this is when *P. barbatus* switches from territory acquisition to production of reproductive offspring.

Because the correlation between diversity and total ants in the community is weak, communities consistently maintain total numbers of ants close to the maximum determined by the parameter values. Although total numbers depend sensitively on the demographic parameters q and σ_D (Figure 4.6), they change relatively little across the different recruitment rates and information collection methods. When the survivorship of workers is low, colony sizes are mostly determined by territory size determined in the spring, allowing colonies to grow to their maximum size in that year because they do not rely on carryover from previous years. With $q = \frac{1}{20}$, individual colonies have longer lifespans, allowing for a more consistent number of large mature colonies in the community. Thus, any death by a colony should be easily filled by a new colony, by neighboring colonies expanding territory or a mixture of both. With a high death rate of colonies ($q = \frac{1}{7}$) total numbers of ants were farthest away from the total theoretical maximum because death of mature colonies allow for more small maturing colonies that have yet to grow to their maximum colony size. Survivorship of workers and colonies over winter was not addressed by this model, but could be included in a stochastic simulation of the community model. This would better simulate a lack of information in the spring experienced by *Tetramorium* ants and possibly be a more realistic simulation of what communities actually experience.

Changes in Simpson's diversity index, a measure of the variability of colony sizes

within a community, can be explained by how efficiently large colonies are utilizing workers to gain territory. Small recruitment rates (ρ) allow for spatial effects to determine more of the territory size because fewer recruited ants will be more easily diluted by distances between nests, especially if those distances are large. Small recruitment rates for the small colonies also increases the pool of recruitable ants in the nest because they will be less likely to be recruited to the battle. Increasing recruitment reduces the spatial effects on the larger colonies, allowing them to better control more of the territory while also reducing the pool of available recruits in the small colonies. This causes more small colonies to drop below either the minimum threshold of workers or minimum territory size. Changing information collection from searching ants to ants involved in dyads effectively slows the rate at which small colonies can recruit to changing battle conditions because dyads must end before recruitment decisions can be made. If information collection is done by the searching class, workers can become motivated and leave to recruit at the same time.

Larger colonies tend to decrease from year to year while small colonies tend to increase from year to year, suggesting that survivorship has a smaller overall effect on small colonies. This makes sense because these small colonies can rebound quickly from the death of workers. Once colonies are established and have gained close to the total territory available to them, small growing colonies could take away some of that territory, but survivorship of workers will have much larger effects on reducing the colony's numbers when they lose more ants than can be replaced from resources in the territory (cT).

In describing the pitched battles of the genus *Tetramorium*, Hölldobler and Wilson [27] state that battles sometimes end in colony fusion. While never seen in my personal observations, this could be added to the model. Instead of disappearing, colonies that lose could be absorbed by larger colonies, summing workers and territory. Whether colonies fuse or defeated colonies are taken over, as in the case of *Myrmecocystus mimicus* [24], it would not affect the model that keeps track of just colony and territory sizes. It would be interesting to investigate how this trait could be used by colonies to grow larger than possible with the current model characteristics. If two large colonies fuse, they could have distinct competitive advantage over neighboring colonies that do not fuse although they could pay the costs of large territories through increased travel times. It is also possible that colony fusion may affect small colonies since two small colonies fusing may be able to

grow to a large colony faster than would otherwise be possible, but a large colony fusing with a small colony may not have any measurable effects since the number of ants and territory added to the large colony may be negligible.

The invasive Argentine ant, *Linepithema humile*, is known for having large supercolonies in their invaded territory. Pavement ants have central place nest sites whereas the Argentine ant has a distributed nest site with cooperation among nests spanning hundreds or thousands of kilometers in Mediterranean climates. These colonies grow to very high densities, giving them a competitive advantage against ants in their native territories [21]. As genetic diversity increases in the territory of the crazy ant (*Anoplolepis gracilipes*), another invasive species that also forms supercolonies during invasions, the supercolony begins to beak down and densities begin to decline [32]. This suggests that there is an inherent cost to territoriality that can be overcome by cooperation between neighboring nests in certain circumstances. The model presented here was unable to address this question since territorial effects were built into the interpolation functions and cooperation between nests was not included in the original battle model. It would be interesting to test if supercoloniality in a similar model is able to exceed the theoretical maximum for a community or how colonies that form nonterritorial groups compete with those that do not.

Table 4.1. Parameters in the community model.

Parameter	Description	Values
σ_D	Worker survivorship each year	0.7 or 0.1
ρ	Recruitment rate	0.000667/min, 0.02/min or 0.04/min
q	Probability of colony death	$\frac{1}{6}$ or $\frac{1}{20}$
ϕ	Information parameter	0 (Searchers) or 1 (dyads)
c	Growth per territory size	60 ants/meter or 100 ants/meter

Figure 4.1. Queen of the genus *Tetramorium* being killed by workers from a nearby *Tetramorium* colony.

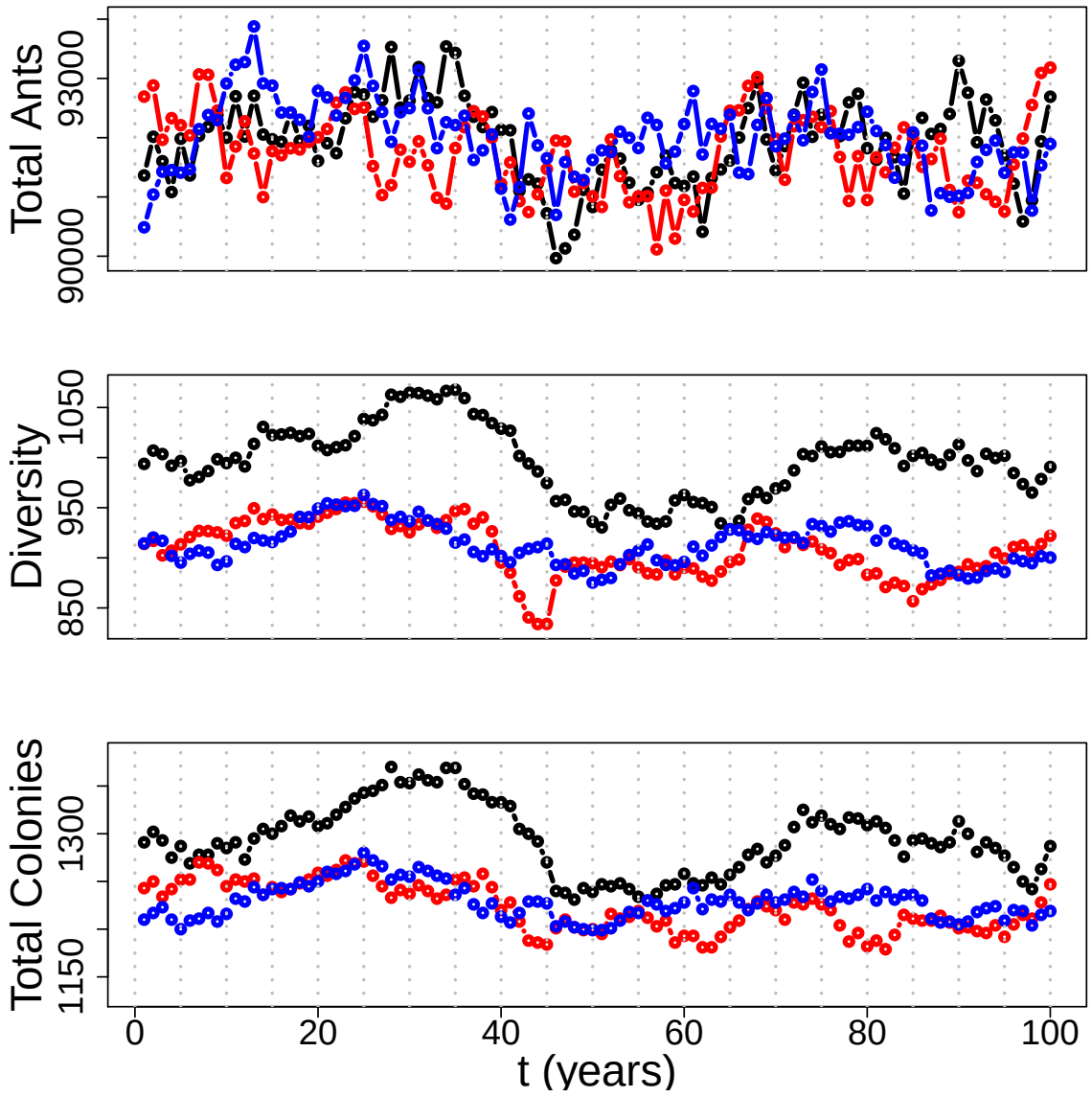

Figure 4.2. Simulation of 100 years for $q = \frac{1}{20}$, $\phi = 0$, $\sigma_D = 0.7$, and $c = 60$. Black indicates $\rho = 0.000667$ ants/min, red indicates $\rho = 0.02$ ants/min, and blue indicates $\rho = 0.04$ ants/min. Theoretical maximum number of ants that can be supported by this community is 100,000 ants.

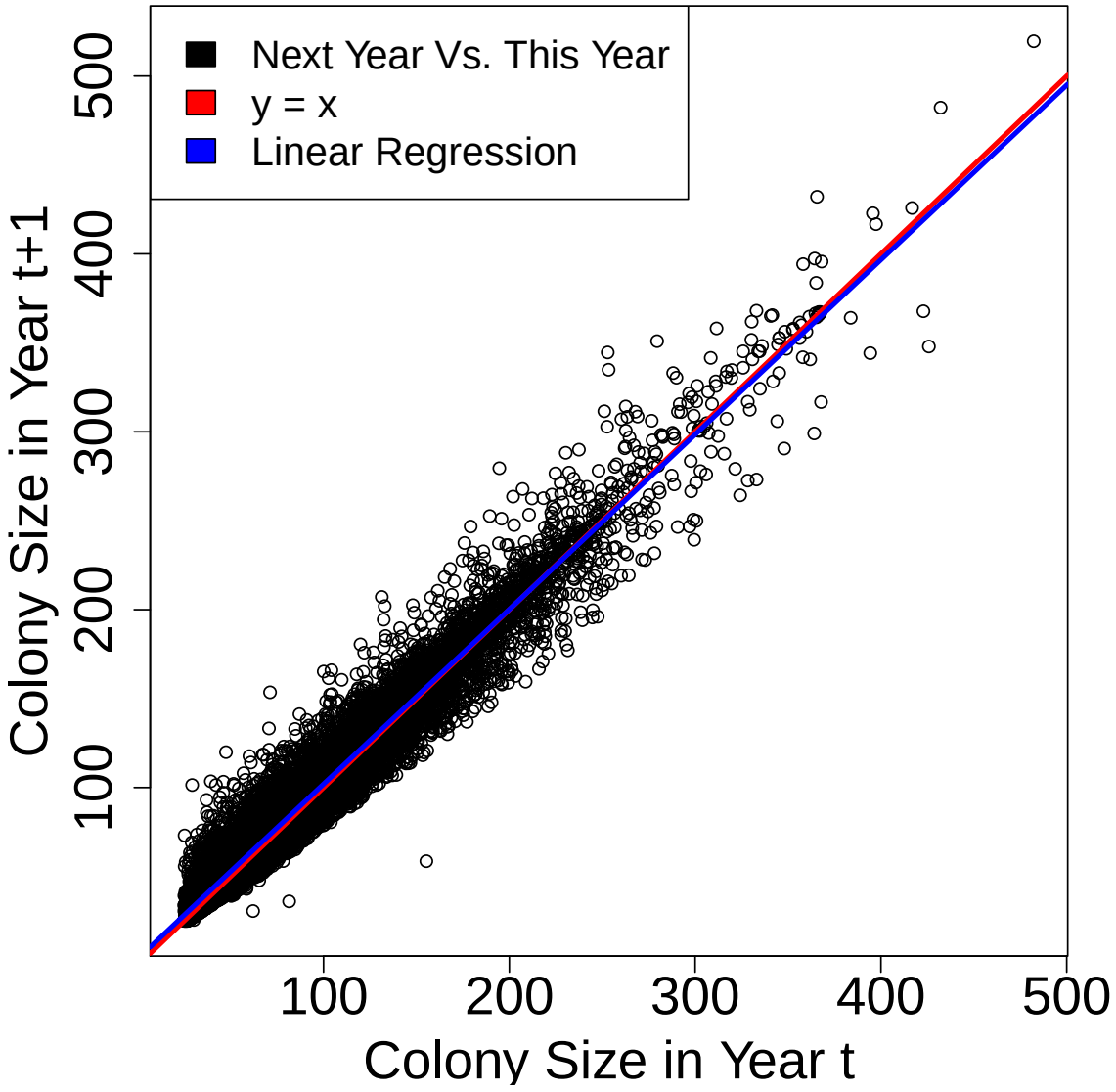

Figure 4.3. Plot showing next colony size versus current colony size. Two lines are $y = x$ (red) and a linear regression of the data (blue). For these data, $q = \frac{1}{20}$, $\sigma_D = 0.7$, $\phi = 0$, and $\rho = 0.04$. Small colonies have a slight tendency to increase and large colonies have a slight tendency to decrease each year.

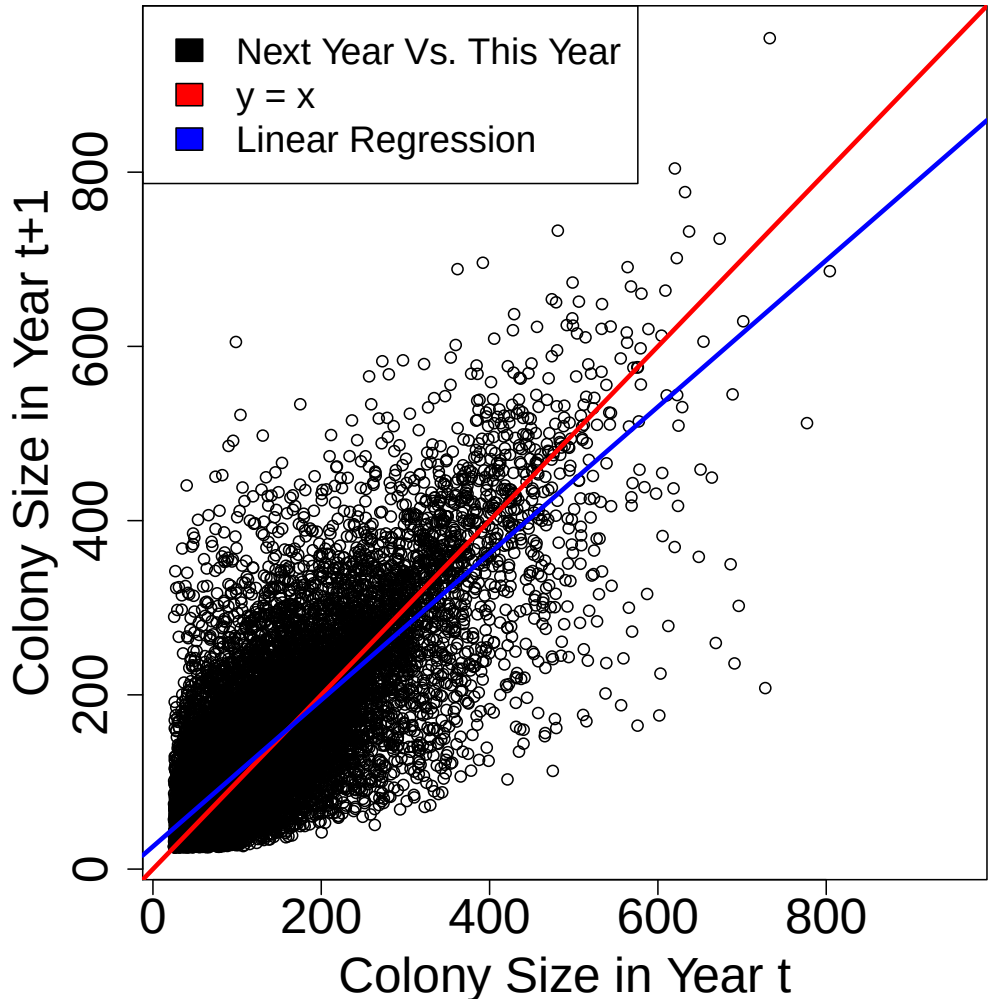

Figure 4.4. Plot showing next colony size versus current colony size. Two lines are $y = x$ (red) and a linear regression of the data (blue). For these data, $q = \frac{1}{6}$, $\sigma_D = 0.1$, $\phi = 0$, and $\rho = 0.04$. Small colonies have a larger tendency to increase and large colonies have a larger tendency to decrease each year than in Figure 4.3.

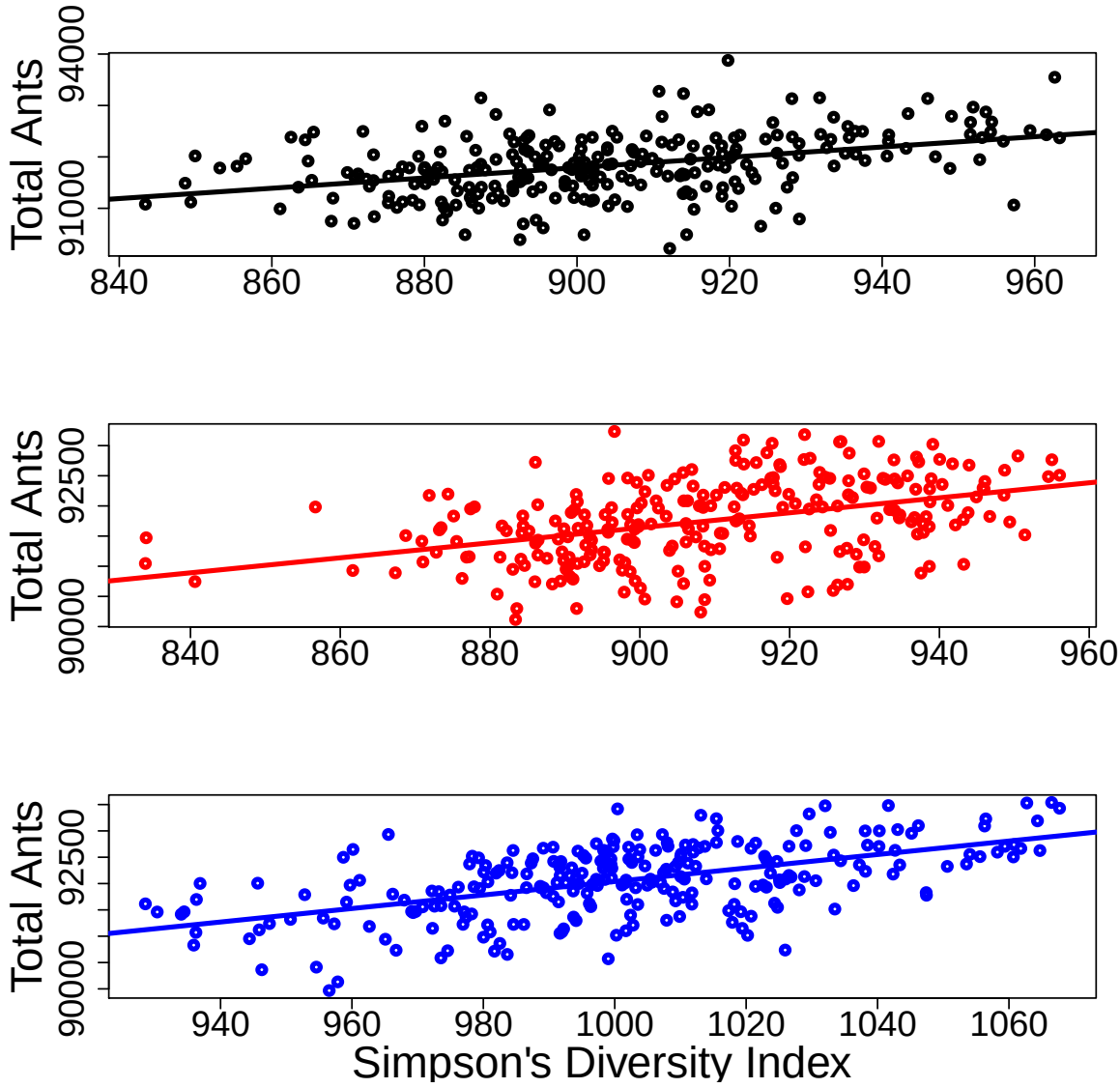

Figure 4.5. Total ants versus Simpson's diversity index. Black indicates $\rho = 0.04$ ants/min, red indicates $\rho = 0.02$ ants/min, and blue indicates $\rho = 0.000667$ ants/min. Lines are linear regressions through the data showing a slight trend that higher diversity leads to more ants in the community. Theoretical maximum number of ants that can be supported by this community is 100,000 ants ($\sigma_D = 0.7$ and $c = 60$).

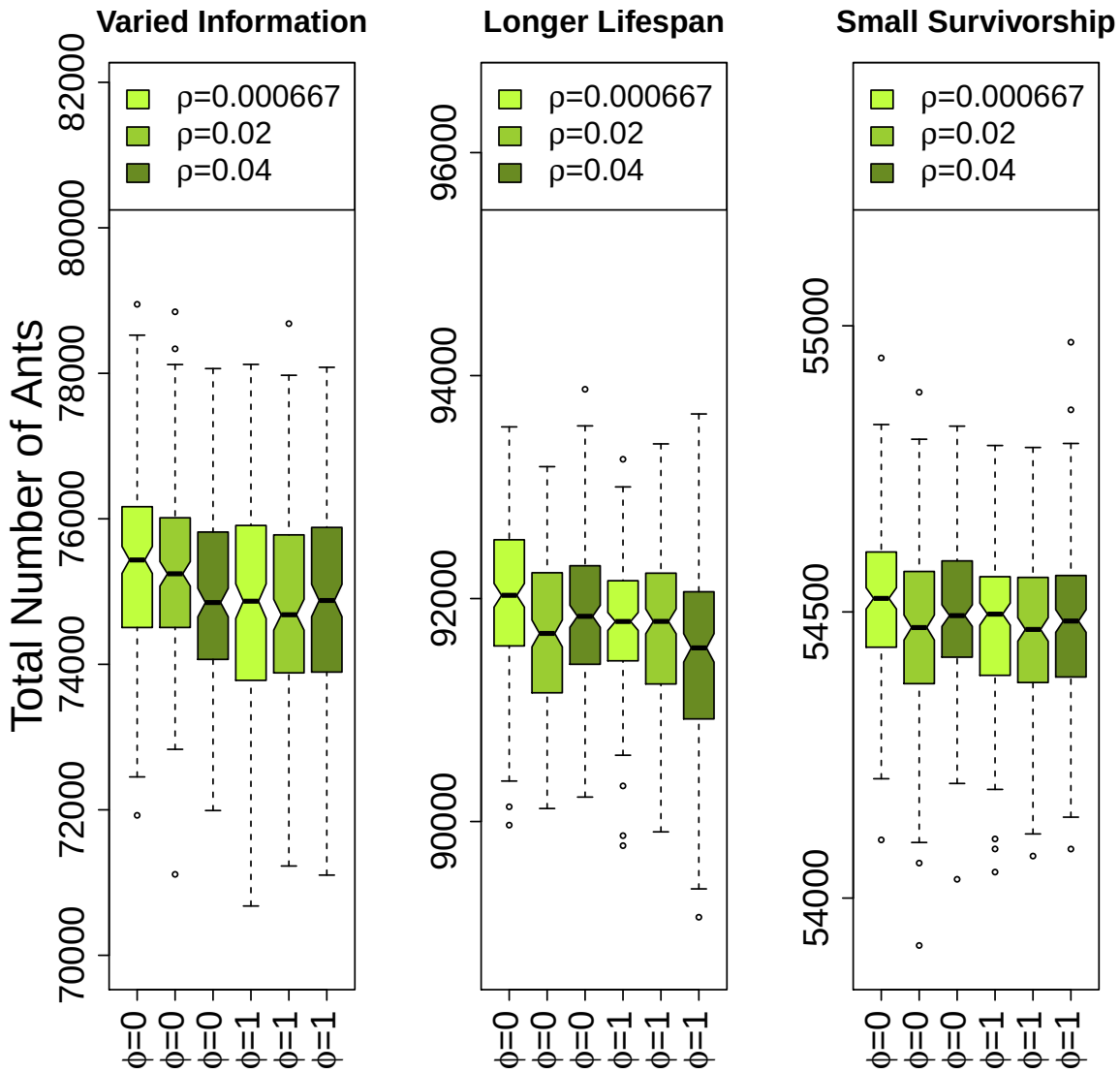

Figure 4.6. Box plot showing the median number of ants with the first and third quartiles. Both ρ and ϕ have no significant effect on total ants.

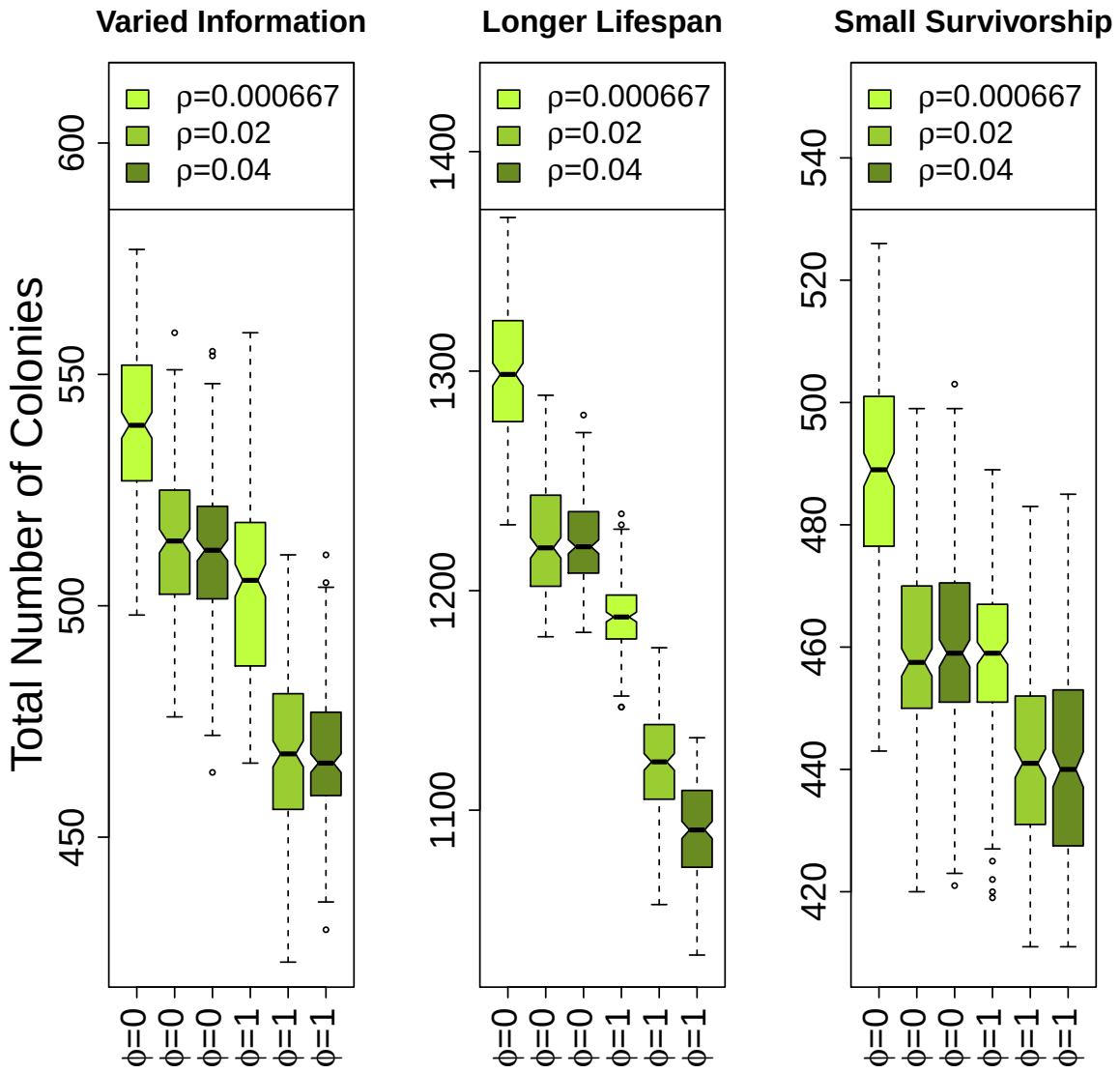

Figure 4.7. Box plot showing the median number of colonies with the first and third quartiles. Total number of colonies varied over recruitment rates ρ and information collection ϕ. The lowest number of colonies for each experiment occurs when recruitment is highest ($\rho = 0.04$) and information is collected by dyadic ants ($\phi = 1$).

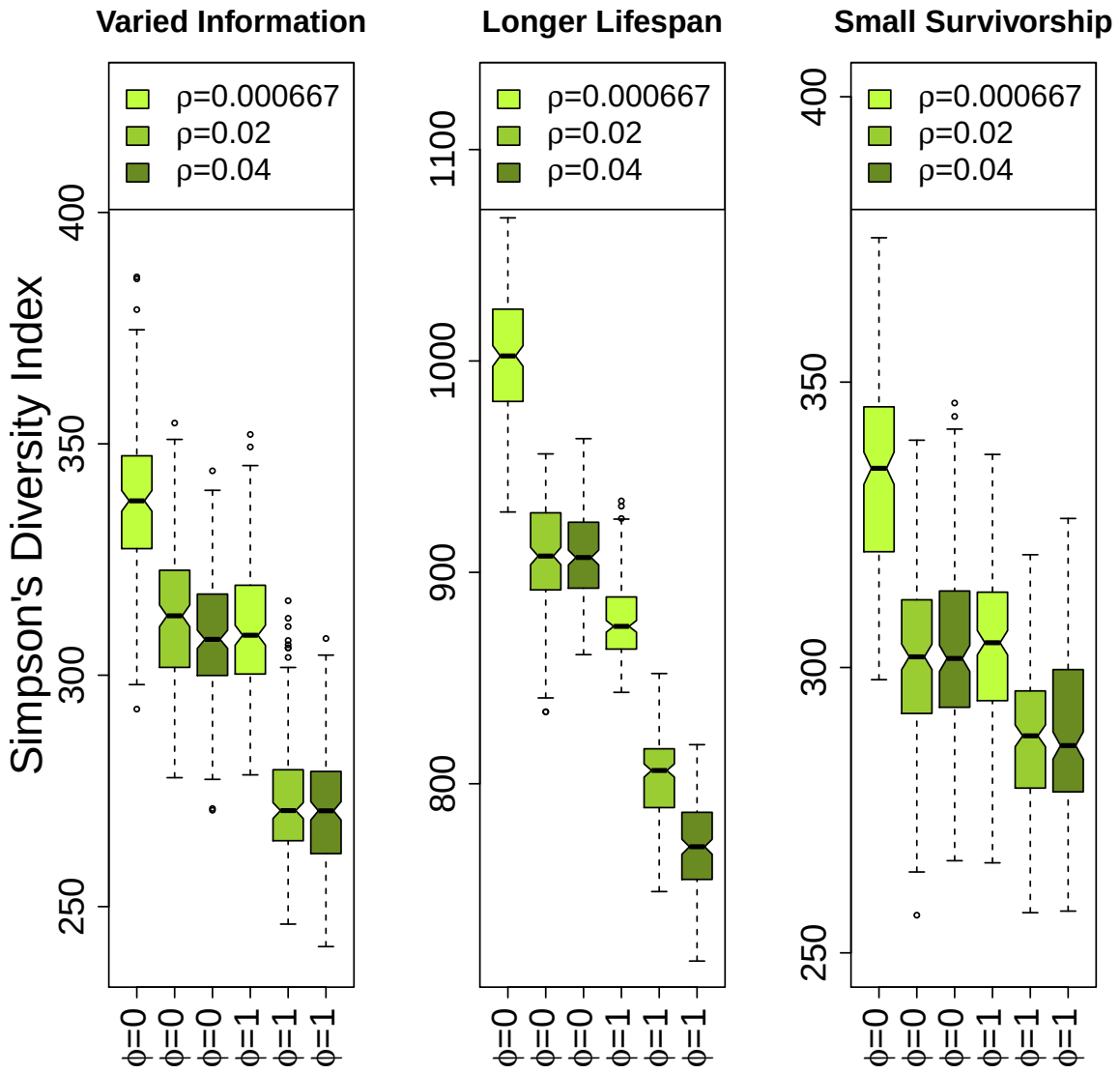

Figure 4.8. Box plot showing the median diversity index with the first and third quartiles. Simpson's diversity index varied over recruitment rates ρ and information collection ϕ. The least diverse result for each experiment occurs when recruitment is highest ($\rho = 0.04$) and information is collected by dyadic ants ($\phi = 1$).

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